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Ecological studies of rhodoliths in Bahía Concepción, Baja California Sur, México

Diana Louise Steller
San Jose State University

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Steller, Diana Louise, M.S.

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U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

ECOLOGICAL STUDIES OF RHODOLITHS IN BAHÍA CONCEPCIÓN, BAJA CALIFORNIA SUR, MÉXICO

A Thesis

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By

Diana Louise Steller

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APPROVED FOR THE DEPARTMENT OF BIOLOGY

Dr. Michael S. Foster, Moss Landing Marine Laboratories

Dr. James T. Harvey, Moss Landing Marine Laboratories

Dr. James W. Nybakken, Moss Landing Marine Laboratories

APPROVED FOR THE UNIVERSITY

ABSTRACT

ECOLOGICAL STUDIES OF RHODOLITHS IN BAHIA CONCEPCION, BAJA CALIFORNIA SUR, MEXICO

By

Diana Louise Steller

The distribution and morphology of rhodoliths was determined in Bahía Concepción, Baja California Sur, México. Subtidal beds of these free-living corallines (*Lithophyllum* and *Lithothamnion*) were up to 1 km in length at depths from 2 to 12 m. Concentration of beds along the western shore of the bay around points and islands may reflect predominant wave direction. Distinct upper and lower bed margins appear to be set by water motion and sedimentation, respectively. Rhodoliths varied in size (1-10 cm), branch density (1-21/cm^2), and wet weight (0.41 - 141.23 g), and these variables generally decreased with increasing depth.

Sampling in one bed revealed temporal and depth related patterns in the distribution and abundance of epiflora, epifauna, and cryptofauna (in rhodoliths). Most organisms (except bluegreen algal/diatom mats) were least abundant when water temperature was highest. The abundance of cryptofauna (9.8±1.2 to 58.4± 7.2/rhodolith) correlated with branch denisty (6.5±.7 to 15.2± 1.2/rhodolith), and both decreased with increasing depth. The infauna in surrounding sediments (predominatly polychaetes) increased with depth. Colonization of artificial rhodoliths suggested that most infauna are attracted to high spatial complexity.

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Chapter 1

Distribution and Morphology of rhodoliths in Bahía Concepción

Introduction

Aggregations of free-living, nongeniculate coralline algae occur on many temperate and tropical continental shelves throughout the world (Adey and MacIntyre 1973, Johansen 1981, review by Bosence 1983b). These generally spherical plants occur from the intertidal zone (Weber-van Bosse and Foslie 1904, Scoffin et al. 1985) to approximately 180 m in depth (Adey and MacIntyre 1973, Minnery 1990, Littler et al. 1991). Living beds are important carbonate producers in nearshore environments and, along with their underlying carbonate sand, have been dredged commercially for use in soil amendment in western Europe for more than a century (Blunden et al. 1975). Variation in shape, branching pattern, and laminar form (layering in unbranched species) have been associated mainly with changes in water motion (Bosellini and Ginsburg 1971, Bosence 1976, Wray 1977). Their morphology affected by wave motion and preservation in fossil deposits allows their use as paleoenvironmental indicators (Bosellini and Ginsburg 1971, Toomey 1975, Scoffin et al. 1985, Prager and Ginsburg 1989, Freiwald et al. 1991). The relationship between morphology, depth, and environment, however, has been debated (Adey and MacIntyre 1973, Reid and MacIntyre 1988).

Since their initial description as corals (Linnaeus 1758), there has been confusion concerning terminology regarding structure, species, and taxonomic position of coralline algae (Woelkerling 1988). This problem is particularly apparent with nongeniculate, free-living forms, often referred to as rhodoliths or rhodoids (Bosellini and Ginsburg 1971, Bosence 1983a, b, c, Norton and Mathieson 1983, Scoffin et al. 1985), and maerl or marl (Lemoine 1910, Cabioch 1966, 1969, Bosence 1976). Rhodoliths or rhodoids are nodules or detached branching growths with a nodular form composed primarily of coralline algae (Bosellini and Ginsburg 1971), nodules with central cores sometimes of stone or abraded coralline (Bosence 1983a), and fragments formed from the fracture and removal of branched encrusting forms (Norton and Mathieson 1983, Bosence 1985). "Maerl" is a

Breton term referring to coralline algal gravels and sometimes includes rhodoliths and their debris (Bosence 1983a). Loose-lying coralline branches or protuberances that break off and continue to grow as free-living plants also are called maerl (Steneck 1986). In geology, the term marl is loosely applied to mixed deposits of calcium carbonate and clay formed under marine or freshwater conditions (Bates and Jackson 1980). The different terms used for these various living forms and their underlying sediments have sometimes been used interchangeably.

Common genera of unattached coralline algae include *Lithothamnion, Lithophyllum, Neogoniolithon*, and *Phymatolithon.* Two distinct growth forms exist: 1) those made almost entirely of branches ranging from compact and dense to open and sparse and 2) those composed of laminar crusts (potentially more than one species) with a central core of foreign material. The branching forms generally occur in shallow water (0-30 m), whereas laminar forms occur in shallow but more commonly in deep water (>40 m; Adey and MacIntyre 1973). The meager available information suggests growth, ecology, and reproduction of these two forms differ (Bosence 1976). Because algal thalli of a few branches to large nodules (up to 10 cm dia. composed primarily of branches) existed in Bahía Concepción, all forms in this study are collectively called rhodoliths.

Rhodoliths occur in diverse environments covering a wide latitudinal and depth range. Intertidal and subtidal (<30 m) aggregations of branching and laminar forms have been described from temperate Norwegian fjords (Freiwald et al. 1991), temperate coastal bays (Cabioch 1966, 1969, Bosence 1976), and tropical island reefs (Weber-van Bosse and Foslie 1904, Bosellini and Ginsburg 1971, Scoffin et al. 1985). Most concentrations growing on deep water shelves or platforms range from 35 to 90 m (Adey and MacIntyre 1973, Fricke and Meischner 1985, Prager and Ginsburg 1989, Minnery 1990). In clear, tropical waters laminar form rhodoliths have been reported growing to depths of 268 m on

sea mounts (Littler et al. 1991). Their wide depth range suggests that a variety of factors may affect their distribution.

Water motion affects rhodolith formation, maintenance of the unattached state, and morphology (Lemoine 1910, Cabioch 1966, 1969, Adey 1971, Bosellini and Ginsburg 1971, Wray 1971, Adey and MacIntyre 1973, Bosence 1976, 1983b, 1985). Steneck (1986) suggested that at any depth, periodic rotation is necessary for light to reach all sides and to avoid burial and fouling, especially if no grazers are present. Toomey (1975) and Minnery (1990) suggested the type of water motion is not important, only that it move the plant. The type of water motion varies with environment and bed depth, ranging from waves and oscillatory tidal currents in shallow beds (Bosellini and Ginsburg 1971, Bosence 1976, Scoffin et al. 1985) to currents, internal waves, and periodic large storm waves in deep-water beds (Toomey 1975, Minnery 1990). Adey and MacIntyre (1973) found that too much water motion broke algal thalli whereas weak waves or currents led to stabilization by growth and coalescence, or burial by fine sediment. Bosence (1983c) reported that aggregations of branching, unattached corallines generally occur in sediment poor areas, sheltered from large waves and strong tidal currents. Oscillatory currents, caused by large waves, broke down banks of unattached corallines (Bosence 1976). Scoffin et al. (1985) found that protection from waves by barrier reefs was crucial for the maintenance of branching rhodoliths around an exposed Pacific island. Tidal currents may be important to turning in these habitats where branching forms develop only in wave protected channels. In contrast, laminar or large nodular forms exist in shallow water with high wave action (Bosellini and Ginsburg 1971), and may survive more exposed conditions than branching forms because mortality from fragmentation would be uncommon.

Alternative factors may contribute to the maintenance of rhodolith sphericity and free-living state under conditions of infrequent repositioning. These include bioturbation

(Prager and Ginsburg 1989), metabolic translocation, and heterotrophic use of dissolved organic material (Littler et al. 1991). Despite these alternatives, water motion is important in most beds, but the range of form, size, and environment of rhodoliths makes it difficult to generalize about water motion requirements.

Light affects growth and geographic distribution of coralline algae (Adey 1966, 1970, Adey and McKibben 1970), and is considered the most important factor controlling coralline depth distribution in the tropics (Adey and MacIntyre 1973). Weber-van Bosse and Foslie (1904) described intertidal knolls of unattached corallines in Haingsisi, Timor "as far as the eye can see," which were not bleached by the sun. In contrast they reported that some Norwegian species lost their pigment during the summer when exposed to permanent daylight conditions. This suggested that high light in shallow water may differentially affect coralline species at their upper depth limits. Rhodoliths generally grow in shallow, protected habitats in turbid northern Atlantic waters, but can occur deeper in clearer tropical waters, often near their photic limit (Adey and MacIntyre 1973). Light may be the primary factor limiting depth distribution of rhodoliths in shallow waters (Bosence 1976, Freiwald et al. 1991), but this has never been tested. Primary productivity measurements of a deep water rhodolith (297 m) indicated an extremely narrow PI curve of net primary productivity suggesting that deep water corallines acclimatize to low light levels (Littler et al. 1991). The wide depth distribution of rhodoliths and their ability to live under various light levels suggests that other factors may influence upper and lower depth limits. The effect of light attenuation on morphology is unknown.

Morphology of individual thalli may reflect variations in water motion and light (Foslie 1894, Lemoine 1910, Cabioch 1969, 1970 1988, Wray 1971, Bosellini and Ginsburg 1971, Adey and MacIntyre 1973, and Bosence 1976, 1983a, b, c, 1985, 1991). Changes in morphology with depth are discussed in the literature (Adey and MacIntyre 1973, Wray 1977), but it is often unclear whether this implies a relationship between morphology and

water motion, light, temperature, or a combination of factors. Where overturning exposes all sides of an alga to light it also results in abrasion of the apical growing tips in branching species. Damage to branch apices results in intercalary or lateral growth, and is reflected in denser branching (Johansen 1981). If repeated branching occurs in one plane, it can give rise to a fan-like branching arrangement (Bosence 1985) or branches anastomize and fuse together. Less rolling, therefore less apical damage allows for pseudodichotomous or apical branch growth and results in more open branched forms (Bosence 1983a). A wide range of forms may occur within a branched species.

Thallus sphericity or variation in form reflects the amount of overturning (Bosence 1976). Employing the maximum sphericity equation of Sneed and Folk (1956), Bosellini and Ginsburg (1971) found that more spheroidal rhodoliths grew in wave exposed areas, where turning was more frequent than in more sheltered areas. Bosence (1976) examined turning rates of different forms in a flume, and found that densely branched, ellipsoidal, or spherical forms were less stable and overturned at lower water velocities than open branched and discoidal forms. Thus laminar or highly branched forms that are spherical may better adapted to high water motion.

Various measurements of relative size, branch density, weight, volume, and sphericity characterized differences in form (Bosence 1976, 1983b, c, Bosellini and Ginsburg 1971, Scoffin et al. 1985, Prager and Ginsburg 1989). Reproducible descriptions of different forms are desirable due to the variation in morphology (Cabioch 1966). If morphology is an indicator of environmental conditions, a general method of classification would allow comparisons of the morphological forms of populations from different areas. Foslie (1894), Lemoine (1910), and Cabioch (1969) used taxonomic form names following species names to characterize growth forms. These names referred mainly to differences in branch density, because Cabioch (1966) and Bosence (1976) suggested this as the main source of morphological variation. To associate the degree of water motion with the types

of forms in an area, Bosence (1976, 1983a, 1985) developed a semi-quantitative method to assign individual plants to groups based on classes of branch density and sphericity. He found that open branched, discoid forms generally occur in quiet waters and dense branched spheroidal forms in exposed locations.

Most studies of living rhodolith beds were descriptive and qualitative with little experimental investigation of the various abiotic factors that may be important for bed maintenance. Rhodolith communities in the eastern Pacific are poorly known. Deep-water unattached corallines were described by Dill (1968) off the California shelf, and Littler (1973) off Hawaii. During floristic surveys in the Gulf of California, Dawson (1960) discovered large beds of unattached species of Lithothamnion and Lithophyllum near La Paz. He also described many unattached species from drift specimens at other locations, attributed their widespread distribution to the quiet, non-muddy waters of the southern Gulf, and suggested that similar beds may be found to be more widespread with further surveys.

The discovery of rhodolith beds in Bahía Concepción, Baja California Sur, México, provided the opportunity for a quantitative description of bed distribution and individual plant morphology. It also allowed for the experimental investigation of the causes of upper and lower rhodolith bed boundaries. My specific questions were: 1) what is the distribution of rhodolith beds in Bahía Concepción?, 2) how does rhodolith morphology vary with depth between and within beds?, and 3) what factors limit the upper and lower margins of beds?

Methods and Materials

Study Area

Unattached coralline algae have been reported in the Gulf of California from Isla Angel de la Guardia in the northern gulf to La Paz in the southern gulf (Dawson 1960). However, Dawson (1960) observed subtidal populations only near La Paz. In this study, large populations were discovered along the western shore of Bahía Concepción (112°W, 27°N), Baja California Sur, México (Fig. 1). The gulf is characterized by distinct seasonal differences in water temperature, nutrient availability, and particularly wind patterns. Water temperature is from 9°C to 22°C, and salinity is 35°/₀₀ to 36°/₀₀ in shallow bays (Alvarez-Borrego 1983). Seasonal winds blow predominantly from the north/northwest from November to May, while from June to October they blow more variably from the southeast from June to October (Alvarez-Borrego 1983, Maluf 1983, Candella et al. 1984a, b, Merrifield et al. 1987; Fig. 2). Bahía Concepción is located on the gulf side of the Baja California peninsula. This 36 km long bay, oriented roughly north/south, ranges in depth from 10 m at the shallow sill near the mouth to 40 m in the southern end. It has a volcanic, rocky shore interspersed with carbonate sand beaches and small, offshore islands on the western side. Waves in the bay result from local winds, although they are influenced by swells arriving from the gulf through the north facing mouth.

Surface water temperature (°C), salinity (°/₀₀ using a hand held refractometer), and secchi depth (m) were sampled on four sampling periods (April 1990, and January, June, and October, 1991) at Isla El Requesón (Fig. 1, bed 5). Wind direction was observed during each sampling period, and compared with seasonal wind data collected for four years at Santa Rosalía, 88 km to the north (Candella et al. 1984 a, b, Merrifield et al. 1987). Swell was estimated during January 1991 by measuring wave height and period.

Sampling

Distribution of rhodoliths beds was observed during an aerial survey conducted in Bahía Concepción on May 28, 1992. Dawson (1960) collected specimens near this area

but did not mention observing any rhodolith beds. The method for detecting beds used criteria established from aerial photos of a known bed at Isla El Requesón. Beds generally have a distinct white band of carbonate sand above their upper, nearshore edges. Below this band is a deeper, dark line denoting the upper edges of the coralline algae. The usually darker sediments bordering the lower edge of the beds were often visible using a polarizing filter. Orientation relative to shore, approximate size, and banding patterns were recorded for all areas having these characteristics. Areas were subsequently surveyed using SCUBA for verification. Some areas not exhibiting these characteristics were surveyed also as a control for the method. Size and shape of the bed at Isla El Requesón was approximated from measurements of water depth around the perimeter of the bed and from transects oriented perpendicular to shore. Nine beds, including the >0.5 km long bed around Isla El Requesón, were sampled to determine depth distribution and examine rhodolith characteristics.

Rhodoliths were identified (Dawson 1960) and verified by J. Norris (Smithsonian). As a result of taxonomic difficulties and morphological variation within a species (Dawson 1960, Woelkerling pers. comm., personal observation), individuals were grouped by morphological differences in the type of branches (blunt or fan-shaped) and not by species (Fig. 3).

Initial descriptions of organism distribution in a bed were made at Isla El Requesón. Two transects, 200 m apart and perpendicular to shore, started 5 m above the upper edge and ended below the lower edge of the rhodoliths. At 1 m intervals along the transects I identified the presence of rhodoliths, foliose algae, animals, or sediment, and whether sediment covered any organisms. Water depth (m) was measured at each point. Clear glass cores (10 cm dia. x 15 cm. depth) were taken randomly through the bed with depth to visually examine rhodolith stacking and the underlying substrate.

To examine the variation in morphology with depth in different beds, rhodoliths were sampled from nine different locations in Bahía Concepción using a depth stratified method

(Fig. 1). Transects (20 m length) were placed parallel to shore 5 m (distance) below the upper margins and 5 m (distance) above the lower margins and at the midpoint between the two (Fig. 4). Because margins of beds occurred at different depths, transect depths varied accordingly. At ten random points along each transect the largest rhodolith within 10 cm was collected and fixed in 5% formalin. A performance curve of longest dimension (X) and branch density (BD) indicated that 10 was an adequate sample size. Beds 1-3, 5, and 7-9 were sampled June 1991, bed 4 in January 1991, and bed 6 in October 1991. Large rhodoliths were sampled because they usually remained intact after collection, fixation, and transportation, allowing for later morphological examination of entire specimens. Large rhodoliths also were collected because the range of sizes present made it logistically impossible to sample the entire population. Conclusions for distributional patterns therefore, were based upon large individuals.

Differences in morphological variables [size (X), branch density (BD), wet weight (WW), see Morphological measurements below] among the nine beds were analyzed with a series of ANOVAs (following log transformation where necessary) with fixed factors of bed location and transect depth (Zar 1984). Before analyses, all data were examined for normality and homogeneity of variance using Cochran's test (Winer 1971). The proportion of rhodoliths occurring in various branching classes (I-IV) also was determined.

To examine the differences in rhodolith morphology within a bed, three sites were sampled at Isla El Requesón in April 1990 (Fig. 4). Sites 1 and 2 were subjected to the predominant swell arriving from the open gulf. They were considered more exposed than site 3, located on the east side of the island Rhodoliths were sampled with cores. Four replicate cores (10 cm dia. x 14 cm deep) were randomly placed along each 20 m transect oriented parallel to shore at upper (4-5 m), middle (6-8 m), and lower (8-10 m) depths of the bed. Core samples were sieved (0.5 mm mesh size) and fixed in 5% formalin for later measurements. Due to possible breakage from coring, only the 10 largest, intact rhodoliths from each core were measured. Because I was not concerned with variation within a core,

the means from the 10 rhodoliths per core were used in subsequent analyses (mean/core, n = 4/transect).

Differences in morphological variables between sites and depths at Isla El Requesón were analyzed with a series of ANOVAs (following log transformation where necessary) with the fixed factors of site and depth. Analyses were done using the mean measurement per core. A Scheffé multiple comparison test was used *a posteriori* when appropriate. The proportion of rhodoliths in various branch density classes (I-IV, see below) was determined for all sites and depths. Differences in rhodolith sphericity with depth were tested using ten randomly chosen rhodoliths from each transect. Sphericity was calculated and plotted on sphericity diagrams (Sneed and Folk 1954).

Depth related size distribution of rhodoliths was estimated from four cores. One core per upper (4-5 m) and lower (8-10 m) transect depth was used from both Site 1 and 3. The longest dimension (cm) of all pigmented and potentially viable rhodoliths, including pigmented fragments ($\geq$1 cm), from each core was measured. Data from the same depth were combined.

Morphological measurements and analyses

All rhodoliths collected were fixed in 5% formalin and then transferred to 70% ethanol. Dimensions of size, branch density (BD), and wet weight (WW) were recorded for all rhodoliths collected. The longest (X), intermediate (Y), and shortest (Z) dimensions, perpendicular to each other, were measured to the nearest 0.1 cm. The X dimension was used a measure of size. A sphericity value was calculated using these measurements in the maximum projection sphericity formula ($(Z^2/XY)^{1/3}$) of Sneed and Folk (1956).

Branch density (#branches/cm^2) was estimated using quantitative measurements and the qualitative class groupings of Bosence (1976). Apical branch tips were counted in five haphazardly placed 1 cm^2 quadrats on each thallus surface and used to calculate the mean number of branches/cm^2/individual. This method does not differentiate between dichotomous or intercalary branching, used to estimate the type of branch damage due to

abrasion from rolling (Bosence 1976). Individuals also were assigned to the class levels (I: sparsely branched to IV: densely branched) used by Bosence (1976). This class method also corresponds to the *var.* designation after the species names used by Lemoine (1910) and Cabioch (1966).

Wet weights (WW) were determined (to 0.01 gm) for 30 rhodoliths from Isla El Requesón, collected randomly at three different depths (5 m, 8 m, and 10 m) and preserved in 70% ethanol. Weight was determined after removal from ethanol and air dried (approx. 20 min.). Dry weight was determined after drying for 12 hours at 60°C. Wet and dry weight were highly correlated (r = 0.987). Therefore, given the number of samples subsequently processed (>900), only WW was measured.

Bosence (1976) considered that wet weight was not a useful characteristic to measure because branches trap sediment and harbor infaunal organisms. Data from rhodoliths collected from the nine Bahía Concepción beds (n=270), therefore, were combined with the April 1990 samples from Isla El Requesón (n=360) to examine the usefulness of wet weight as a descriptive morphological character and its relationship to other variables. Regressions were conducted using the independent variables of X, BD, and the relationship between spherical volume (using X, Y, and Z), and BD against the dependent variable of WW. Data were log transformed where appropriate. The relationship between variables used was:

$$\text{WW (gm)} = \text{volume (V)} \times \text{branch density (BD)}$$

$$\text{Where} \quad V = (4/3\ \pi r^3)$$

$$r = 1/2\ \left(\frac{x + y + z}{3}\right)$$

$$BD = \#/cm^2$$

Because of obvious differences, two groups were designated based on gross branch morphology: "blunt-branched" and "fan-branched" (Fig. 3). As branch type may be associated with species differences the percentage of individuals in each branch group was

determined for each bed location. All rhodoliths sampled were examined for presence of conceptacles but reproductive state (spermatia, carpo-, tetra- or bi-spore, or whether gametes or spores had been released) was not determined.

Experiments

To examine factors limiting the upper and lower distribution of beds, and rhodolith movement and growth, in 1991 a series of experiments were done at Site 1 at Isla El Requesón. To determine the fate of rhodoliths beyond their upper and lower distributional limits, in January 1991, three square 50x50x6 cm piles of rhodoliths were placed 1 m above the upper (3.8 m depth) and 1 m below the lower (12.3 m depth) bed margins. A stake in the center of each square served as a reference point. Daily observations were made on the piles. Shape of the pile, dispersion (cm), and rhodolith condition (pigmentation, fouling) were noted daily for the following three days and again in June 1991.

The effect of depth on movement and turning was examined using tagged rhodoliths. Forty rhodoliths of similar size ($x \pm S.E. = 5.28 \pm 0.51$ cm) and branch density (~16/cm^2) were collected from a depth of 5 m and tagged with colored wire. Ten were equally spaced in a 20-cm diameter circle, at 4, 5, 6.5, and 11.3 m depths between the upper and lower margins of the bed. A stake was placed in the middle of each circle as a reference point. The distances between rhodoliths and stakes were measured at three times; day one (T1), 2.5 days (T2), and 5 (T3) days after placement.

To examine the effect of limited movement on rhodolith condition, three 1 m^2 nets were used in January 1991 to restrict rhodolith movement. The one cm mesh monofilament nets were placed directly over the bottom at 4 m depth, and held with stakes at the four corners. This limited the movement of the rhodoliths underneath to slight jostling against each other. Percent cover of associated flora, fauna, and rhodoliths was estimated in the three 1m^2 netted areas and in three nearby randomly located 1m^2 control quadrats using a random point quadrat method (20 points/net; Cowen et al. 1982). Sampling was done in June

1991, the nets cleaned of all fouling, and the areas sampled again in October 1991. After testing for normality, homogeneity of variance (Winer 1971), and arcsin transformation, a t-test was used to compare total percent cover of rhodoliths (or unfouled area) in netted and control quadrats for the last sampling date in October 1991.

I tried to estimate coralline growth rates during 10 months. Four blunt-branched rhodoliths (Lithothamnion australe), were epoxied to PVC stakes 20 cm off of the bottom at 4.6 m, 6.1 m, and 10.7 m depth in the bed in January 1991. Four fan-branched forms of Lithophyllum diguetii and Lithophyllum veleroae also were placed on stakes at 6.5 m. Initial sizes were the average of the X and Y dimensions. Individuals were measured again in June and October 1991. Percentage cover of fouling organisms on the surface of these rhodoliths was estimated using 10 random points on the rhodolith surface for all treatments in June and October 1991. Fouling organisms were removed after the June sampling. The surface of four randomly selected, unstaked rhodoliths from the same depths were sampled as controls. After arcsine transformation a Model I ANOVA was used to test whether percentage fouling was different for depth and treatment for the October 1991 sampling.

Results

Twelve rhodolith beds, up to 1 km in length, were identified during the aerial survey. All beds were located along the lower western shore of the bay and on the northern and southern sides of some offshore islands (Fig. 1). A margin of white carbonate sand bordering the volcanic rocky shore was the most visible character distinguishing most beds. Carbonate sandy beaches were sometimes located nearby. Only one bed, not seen from the air, was found while diving. It was obscured by a floating mat of a netlike brown alga, *Hydroclathrus clathratus* (C. Ag.). Rhodoliths underneath the mat were more pigmented than individuals outside. Although rhodolith beds mainly occurred around distinct geographic points and islands, the largest, discontinuous beds were situated along straight stretches of the coast (beds between 3 and 4, Fig. 1). Mangrove swamps and river beds occurred between some of the rhodolith beds. Rhodolith beds were approximately 200 m to 1 km in length (horizontal distance along the shore) and 30 to 130 m in width. The rhodolith bed around Isla El Requesón was approximately 0.2 km^2, with a maximum width of 130 m. Ripples of living rhodoliths were present at the tapering ends and the upper margins of some beds, with rhodoliths on the crests and carbonate sand in the troughs At the south end of Isla El Requesón ripples oriented southeast to shore were 3 m wide and 3 m apart, with a height of approximately 40 cm.

Surface water temperature at Isla El Requesón was 18.5 °C (January 1991) to 29.5 °C (October 1991), salinity 35.0 to 36.5°/oo and secchi disc readings increased from 6.5 to 9 m (Table 1). The predominant wind directions were similar to those described by Alvarez-Borrego (1983) and Candella et al. (1984a and b; Fig. 2). In January 1991, strong winds blew from the N/NE and wave swell direction was from the north. The largest waves were 1 m in height, a length of 7 to 10 m, and period of 2 to 3 seconds. During June 1991, winds were weak and highly variable, switching daily from N to SE. There were only slight breezes and no swell in October.

Five species of algae were found in the rhodolith beds, and all were entirely branched (no non-coralline material). These fruticose or "bush-like" algae, composed primarily of non-geniculate protuberances, were placed into very general morphological groupings based on branch type (Fig. 3). "Blunt branched" types had rounded, mammalated, distinct apical tips that were sometimes anastomized. "Fan branched" types had flattened, undulating branches that grew as or were anastomized into plates like a fan. Based on Dawson (1960), species associated with these morphological groups were:

"Blunt branched"	-*Lithothamnion australe*	(Foslie) Foslie
	-*Lithophyllum pallescens*	(Foslie) Heydrich
	-*Lithophyllum margaritae*	(Hariot) Heydrich
"Fan branched"	-*Lithophyllum diguetii*	(Hariot) Heydrich
	-*Lithophyllum veleroae*	(Dawson)

Rhodolith beds generally had distinct upper and lower limits, and algal morphology varied with depth at most sites (Fig. 5). The rhodoliths exhibited a wide range of sizes (1 to 10 cm diameter), branch densities (1 to 21/cm^2), and wet weights (0.41 to 141.23 g). The upper edge of living rhodolith beds generally started below a band of coarse carbonate sand made primarily of fragments of dead algal thalli. This upper region was characterized by spherical, densely branched rhodoliths that covered up to 100% of the bottom, and were sometimes stacked two to three individuals deep. Size and branch denstity generally decreased with increased depth. Underlying the living material was carbonate sand and anoxic sediment. Rhodoliths generally ranged from densely compact to sparsely open branched forms, and fan and blunt branched forms were found in all beds. Individuals of *L. diguetii* and *L. margaritae* were generally lighter and more sparsely branched forms and

concentrated at lower transect depths. *Lithophyllum pallescens*, *L. australe*, and *L. veleroae* exhibited a wider range of forms and were found at most transect depths.

A variety of other plants and animals were found on the surface and in the branches of rhodoliths. Surface taxa included sponges, tunicates, bivalves, and a variety of foliose algae, and these varied with depth and time of sampling (see Chapt. 2). The most abundant fish associated with the bed, *Paralabrax maculatofasciatus*, was observed foraging for invertebrates and disturbing rhodoliths. Near the lower limit, rhodoliths were usually more sparsely branched, covered less of the bottom, and were covered with a layer of fine sediment. Fine sediment continued beyond the lower edges. This pattern was observed in most beds although there was considerable variation in the depth of the edges (Fig. 6). Depth of the upper edges generally decreased with increasing distance from the mouth of the bay, but there was no such pattern in the lower edges.

For beds 1-6, rhodoliths generally were larger, more densely branched, and heavier at shallow depths and smaller, less densely branched, and lighter with increasing depth (Fig. 7). There was a significant two-way interaction between beds and depths ($p<0.001$) for all variables (Table 2).

The rhodoliths sampled from the nine Bahía Concepción beds were in branch classes III and IV (Table 3). At most beds and transect depths, a decrease in BD with increase in depth (Fig. 6B) corresponded to a shift from class IV to III (Table 3). A change in BD did not, however, always reflect a change in classes as class IV designations included branch densities ranging from 8-20/cm^2. Eleven percent of rhodoliths collected from all locations and depths in Bahía Concepción were fan-branched.

At Isla El Requesón, all morphological variables, except BD at site 1, decreased in magnitude with increased depth. Rhodoliths were generally larger and more dense at site 1 (Fig. 8). There were no significant interactions between depth and site (Table 4). Rhodoliths were significantly smaller at lower depths (*a posteriori* Scheffé test). The

majority of rhodoliths in the upper depths of the sites were class IV, and classes III and II increased in deeper water (Table 5). The proportion of rhodoliths in class IV decreased from site 1 to 3 in the middle transects. Sixteen percent of rhodoliths from all depths and sites (n=360) were fan-branched.

Rhodoliths were 1 to 5.6 cm diameter, but most individuals were small (1-2 cm) for both upper and lower depths (Fig. 9). Although there was a wider range of sizes at the lower depth (1.0-5.6 cm; Fig. 9b), a greater number of large plants were present at upper depths (Fig. 9a). There were more rhodoliths ($\geq$ 1 cm) in cores at 4 to 5 m depth (n=257) than at 8 to 10 m depth (n=102).

At all three depths in the bed most rhodoliths were spherical (Fig 10). Plants became slightly less spherical with increased depth, as indicated by the greater number of individuals below the 0.5 indicator line.

Longest dimension (X) was highly related to WW (r^2=0.759) but branch density (BD) was not (r^2=0.157; Fig. 11). Wet weight was best estimated using spherical volume times the branch density (r^2=0.892). For the X variable more dispersion occurred as weight increased.

In June and October, 1991, the lower portion of plants were visibly more pigmented than the upper, exposed surfaces. Similarly, rhodoliths under the H. clathratus mat in June were more pigmented then individuals not under the mat. During October 1991, all but the upper portion of the rhodolith bed at Isla El Requesón, was covered with a blue-green algal/diatom mat (approx. 0.5-1.0 cm in depth). Rhodoliths underneath were more pigmented than those not covered and noticeably more brittle. This occurred when water temperature, clarity, and salinity were greatest (Table 1).

Reproductive structures were present at all sampling dates and sites in 1990 and 1991. Percentage of rhodoliths with conceptacles varied from 3.3% to 26.7% per bed (n=30/bed). Conceptacles were visible on thalli collected at Isla El Requesón during every

sampling period (April 1990, 12.9%, n=360; January 1991, 25.8%, n=120; June 1991, 14.4%, n=90; and October 1991, 21.2%, n=90). In general conceptacles were concentrated on the sides and near the tips of branches or protuberances.

Experiments

Movement and transplant experiments indicated that the bed at Isla El Requesón was more dynamic at upper than lower edges. After one day, the three rhodolith piles beyond the upper edge of the bed were dispersed, only circular piles of intact and broken rhodoliths, ~20 cm radius, were around the stakes. After two days each pile was spread into a 1 to 3 m long band in a SE direction, perpendicular to the dominant NE swell. During the same time, the lower piles maintained their square form but were lightly covered with silt and drifting foliose algae. On day three, a few rhodoliths in the shallow piles were in circles of an average 10 cm radius around the stakes, the remainder were dispersed in a fan shape away from the stakes. Lower piles were still in their original shape covered with silt. Slight movement in the lower piles apparently resulted from bioturbation by sea cucumbers (*Isostichopus fuscus*). In June 1991, five months after the initiation of the experiment, the stakes of the upper piles were found but live rhodoliths were completely dispersed and could not be distinguished from the surrounding sand. The lower piles were dispersed within 1 m of the stakes and covered with a layer of sediment 2-5 cm in depth. These rhodoliths were generally intact but bleached. Some branches were black from anoxic conditions beneath the sediment, and branches were missing.

Little wind or swell was present for the first 24 hours of the turning experiment, and no movement was observed at T1 (Table 6). Between T1 and T2 the wind blew from the northeast and the swell increased to a height of 1 m with a wavelength of 7-10 m and a period of 2-3 seconds. The wind and swell continued between T2 and T3. Rhodolith displacement occurred at all depths by T2 and T3, with a gradient of decreasing movement with increasing depth.

The restriction of rhodolith movement with nets resulted in no significant differences in the cover of rhodoliths between netted areas and controls for any sampling date (Jan., $t = 0.361$, June, $t = 0.252$, Oct., $t = 0.259$, $t_{0.05,(2),4} = 12.2$; Table 7). Cover of associated organisms, including anemones, sponge mats, and foliose algae was low and variable during both sampling dates on treatments and controls. In October bluegreen algal/diatom mats fouled the nets in the experimental plots but not the rhodoliths. During June and October, rhodoliths (approximately 20) were resting on top of the nets.

Rhodoliths on stakes in growth experiments became fouled with sponges, tunicates, and algae, making most growth measurements inaccurate. Individuals staked at the lower transect were not fouled in June and the mean calculated growth rate was 0.93 mm/month (n=2; two of the lower depth rhodoliths were broken and not included). The percent cover of organisms fouling initially clean rhodoliths was calculated in June and October 1991 for the blunt-branched rhodoliths (Table 8). There was no significant interaction between treatment and depth on fouling in October 1991. Although fouling was not significantly different among depths, staked rhodoliths were more highly fouled than controls. There was an increase in fouling from June to October.

Discussion

The discovery of thirteen shallow-water rhodolith beds in Bahía Concepción verified the presence of large unattached coralline beds in the Gulf of California north of La Paz as predicted by Dawson (1960). The concentration of these *Lithothamnion* and *Lithophyllum* beds in the southwestern part of the bay and on the north and south side of islands suggests that the oscillatory water motion resulting from predominant wind and swell direction is important in the development and maintenance of rhodoliths in the confined waters of this bay. Orientation to local winds and swell, and variation in sediment accumulation with depth appear to influence geographic distribution, bed size, depth distribution, and overall rhodolith morphology. Dissipation of focused wave energy with depth and distance away from geographic points and islands may limit rhodolith turning enough to produce discontinuities in bed distribution and limit bed size. Too much water motion breaks thalli down, whereas reduced wave or current action could lead to stabilization or burial by fine sediment (Adey and MacIntyre 1973). Input of fine sediment from near shore mangrove forests and river beds also may contribute to bed discontinuity. Beds did not occur at all points or islands, although some of these locations had depth profiles and orientations similar to those with beds. This may be due to a lack of coralline source material to initiate bed formation, or, more likely, to variations in abiotic factors that were not observed during the limited surveys.

Water motion, sedimentation, and light limitation are all abiotic factors that may affect rhodolith bed distribution. Ripples of live rhodoliths and carbonate sands concentrated at the longshore margins indicated that excessive or insufficient wave energy contributes to bed discontinuity. The rapid displacement and breakdown of rhodoliths moved above their upper limit at Isla El Requesón strongly indicated, as suggested by Adey and MacIntyre (1973), that the upper limit is set by water motion. High levels of light could limit growth at the upper edge, but this is unlikely as some beds were very shallow (2 m) and plants

were generally more robust at shallow depths (Fig. 6). Moreover, unbleached intertidal rhodoliths have been reported elsewhere (Weber-van Bosse and Foslie 1904, Scoffin et al. 1985, Freiwald et al. 1991). Although sedimentation rates were not measured, complete coverage of rhodolith piles below the lower bed margins suggests sedimentation sets the lower limits, at least at Isla El Requesón. Although local sedimentation and reduced water motion may increase turbidity and light attenuation, thus potentially limiting depth distribution, this is unlikely. The minimum 6 m secchi disk readings indicated light intensities were greater than 1% of surface irradiance at depths above 18 m (Holmes 1970). This should maintain growth beyond the 12 m depth maximum of the deepest bed. Corallines can survive burial for some time and survive shading by carbohydrate storage (Steneck and Adey 1976). This depends upon rhodoliths being uncovered, a phenomena not observed at the lower limits of the Isla El Requesón bed. Although these experiments were conducted only at one site, the similarities of conditions at the upper and lower margin at other sites in the bay, and similar general descriptions of rhodolith requirements by Adey and MacIntyre (1973) indicated water motion and sedimentation may generally limit bed size.

Variation in depth among beds may indicate variation in water motion, turbidity, light, and sedimentation within this relatively small geographic range. It is unclear which factor(s) influenced the decreasing depth of the upper margin with increased distance into the bay (Fig. 5). Swells generated by NE winds may increase towards the south of the bay as fetch increases, increasing surge depth and decreasing upper margin depth. The seasonal SE winds may also influence upper limits by producing short period waves from the south resulting again in high water motion in shallow water. Under both conditions, however, beds on opposite sides of islands would be exposed to different water motion regimes. This distributional pattern could be further examined by measuring the depth of all beds, and with more complete, site specific information on winds and swell. There was

no trend of depth of lower margins with distance down the bay. This variation may result from the combined affect of differential water motion, slope, local sedimentation, and turbidity, but remains to be examined.

Although it appeared that changes in plant morphology with depth were primarily due to changes in form not species, it was not possible to determine the overall species distribution along depth gradients due to difficulties in coralline identifications. Individuals of *Lithophyllum diguetii* and *Lithophyllum margaritae*, which were generally less branched, may be concentrated at deeper depths as survival may decrease with higher turning frequency at shallower depths due to thallus breakage. The wider range of forms expressed by *Lithothamnion australe*, *Lithophyllum pallescens*, and *Lithophyllum veleroae* may enable them to extend over a greater depth range. Species of nongeniculate corallines in the gulf have not been evaluated since the work of Dawson (1960). In his key, species differences were based largely upon the morphological differences in size and shape of branches and protuberances, texture of the vegetative surface, and conceptacle size. Woelkerling (pers. comm.) indicated that corallines of Pacific Mexico need reassessment because differences in morphology are considered of limited taxonomic significance and too variable to be reliably used (Woelkerling and Campbell 1992). Dawson (1960) also suggested that forms were highly variable within a species (pg. 71, Plate 4). It is likely that "blunt" and "fan" branching groups are different species but given the range in forms, with better taxonomic evaluation some of the species within these groups may be combined. Trends in morphology are still evident and presumably reflect environmental conditions whether they are due to species differences or forms.

Depth related trends in rhodolith form, particularly branch density (Figs. 6, 7) were similar at most beds despite variation in transect depths between beds. The general trend, decreasing size, branch density, and wet weight with increasing depth, was detected over a relatively small depth range (2-5 m) and among beds. This suggests that factors

influencing morphology have a similar influence in different beds. Variation in form is primarily influenced by variations in water motion (Lemoine 1910) and factors changing with variation in water motion and depth (Wray 1971, 1977, Bosence 1976). Bosence (1976) suggested that increased turning abrades the surface producing greater branch density due to increased lateral, intercalary branching. A decrease in turning and abrasion, sometimes associated with increased depth, may allow for lower branch density resulting from apical branch growth with dichotomous branching. Although the high wet weight of more branched individuals may be influenced by increased infauna and sedimentation, rhodoliths in Bahía Concepción had little associated sediment, and animal weight was relatively small relative to the rhodolith. Therefore, higher weight is generally a result of size and more branch material/volume. Cabioch (1969) and Bosence (1976) indicated that reduced movement, along with reduced light and increased sedimentation in deeper water facilitates increased growth of apical branches resulting in lower branch density. Large scale variations in the distribution of forms has also been related to sediment type. Cabioch (1969) found highly branched individuals grew on coarse grained sediments and sparsely branched forms on fine grained, muddy sediments. Cabioch (1969) collected with dredges, so little is known about the relationship between depth, water motion and sedimentation. In most previous studies there were few data concerning area or depth differences over which morphological changes occurred. Depth stratified transects in this study were useful in detecting the high variability in form that occurs over small spacial scales in most beds.

Not all morphological variables decreased with increased depth in all beds in Bahía Concepción. In some rhodolith beds, size, branch density, and weight increased with depth or were greatest at mid-bed (Fig. 6). This may reflect variations in exposure or sorting of individuals within a bed. Freiwald et al. (1991) described open branched rhodoliths in the intertidal and more nodular and densely branched forms in deeper water

(15 m) in Norwegian fjords. This pattern is opposite that of most other reports, and may be due to deep currents in fjords and a calm intertidal zone. Therefore, when generalizing about the factors influencing thallus form of free-living corallines, the assumption that water motion decreases with increasing depth (Wray 1977) can be misleading. In simple models relating the influence of overturning on thallus form, it is better to incorporate a measured rate or frequency of overturning (Adey and MacIntyre 1973) than assume this rate declines with depth.

Bioturbation from crustaceans, echinoderms, and fish causes rhodolith overturning (Bosence and Pedely 1982, Prager and Ginsburg 1989, Minnery 1990). I observed bioturbation by the cucumber *Isostichopus fuscus* during the transplant experiments, and by fish (primarily *Paralabrax maculatofasciatus*) that moved the plants while foraging for invertebrates. Although cucumbers or fishes may overturn rhodoliths, their influence in Bahía Concepción is considered minimal compared to water motion.

There was high variation in rhodolith size, branch density, and wet weight among the nine beds. High morphological variation was also observed among sites in one bed at Isla El Requesón where differences in form occurred over relatively small horizontal distances and where transects were at similar depths. Although not statistically significant among sites, rhodoliths at Isla El Requesón were larger and more highly branched at site 1 and smaller at sites 2 and 3. These data suggest that larger rhodoliths grow in areas with higher exposure to predominant wind and swell direction. However, this is difficult to determine because rate of abrasion and influence of age on size is unknown. Similar depths were sampled at each site making it unlikely that changes in light influenced the observed differences. Differential exposure affecting both turning and sedimentation rates, appeared to be most responsible. This among site variation in one bed may help explain the more distinct, large scale differences between beds in Bahía Concepción. The high variation in exposure, depth distribution, and thallus forms among beds indicated abiotic factors

inherent to particular beds influence morphology. Although the significant interactions between site and depth for all morphologic variables measured in Bahía Concepción beds make interpretation difficult, the F-ratios (Table 2) indicate that size may be most affected by factors that vary among beds, whereas branch density and wet weight are most affected by factors that vary with depth.

In this study two methods (largest individual near a random point and cores) of sampling rhodoliths were used. Similar depth-related patterns resulted for all variables when both methods of sampling rhodoliths were used at Isla El Requesón (Fig. 6, bed 5; Fig. 7). Values of BD and WW were higher using the largest individual near a random point than cores. More smaller individuals were sampled using cores; therefore, means of 10 rhodoliths in cores were less than values derived using the largest individuals. Similar trends between the two methods, however, suggested that although sampling only large individuals does not allow interpretation of the entire population, it does reflect overall distributional patterns when combined with depth stratified sampling. Most living material in cores was 1 to 2 cm fragments and the higher number of individuals from shallow water cores reflects the higher thallus fragmentation at these depths. Survivorship and growth of fragments is unknown indicating the importance of focusing on larger individuals to examine morphological trends.

Spheroidal and ellipsoidal plants are considered forms that live under high energy conditions (Prager and Ginsburg 1989), are easily transportable (Bosence 1976, 1983c), and grow on open gravels where the thallus is supported by other individuals, allowing for lateral growth. The predominance of spheroidal forms in the bed at Isla El Requesón indicated frequent turning. The slight decrease in sphericity in deeper water may result from less turning and increased apical, elongate branch growth with increased depth. However, it is difficult to compare the depth-related distribution of forms at Isla El Requesón with those of other studies because different workers have used different

sphericity equations. Sneed and Folk (1956, p. 18) defined maximum sphericity as the cube root of the square of the shortest axis divided by the product of the longest times the intermediate axis. Bosellini and Ginsburg (1971) first applied this formula to rhodoliths and plotted results on the sphericity form diagram but report the maximum sphericity as the square root of the same combination of axes even though they cite Sneed and Folk (1956) as the source for the relationship. As the raw data are not included in these reports it is difficult to determine where the errors occur and how to compare results. While differences in sphericity may reflect different water motion, it is difficult to generalize about the distribution of forms based on differences in water motion because of discrepancies in determining shapes.

Bosence (1983c) suggested that wet weight is not a useful variable, because it varies with amount of material trapped among branches. Correlations between wet weight, size, and branch density, however, indicate that wet weight also may reflect the effects of environment on morphology. The high correlation between wet and dry weight, and wet weight and (volume)x(branch density) further indicated wet weight may be a good indicator of changes in form and may be predictable from measures of size and branch density. The poor relationship between wet weight and branch density may reflect the wide range of rhodolith sizes with similar branch density. Wet weight is a useful, and quick variable to measure to roughly estimate differences in form.

Branch density and classes of branch density reflected similar depth-related patterns in rhodolith form. Although assigning a class level is faster, it is qualitative and provides an approximation of form, however, it does not reflect the fine-scale variations evident in Bahía Concepción from counting the number of branches/cm^2. Counts produce a more quantitative measure and should allow more detailed statements about environmental variation in paleoecological interpretations if this character is preserved. The high proportion of individuals in class III and IV (Tables 3 and 4) may have resulted from

sampling only large individuals. The presence of more individuals in class II at Isla El Requesón when using cores (Table 5) probably reflects the wider range of population sizes sampled with cores.

Fouling by bluegreen algal/diatom mats and macroalgae during times of high temperature and light may benefit corallines by providing shade and nutrients. Some corallines survive when fouled by filamentous, leafy, or fleshy algae (Adey 1966). As there are no prior data from this area, it is unknown whether these mats are common during late summer. However, mats of bluegreen algae often form extensive subtidal mats over the bottom during periods of high temperatures (Humm and Wicks 1980). The unfouled upper portion of the bed during October 1992 indicated recent rhodolith movement at the shallow depths. The apparent brittleness of the algae at this time could be from calcium or pigment loss associated with high light and temperatures and low nutrients measured during 1991 (Martinez-Lopez et al. 1992). In April 1992, the bed appeared the same size and rhodoliths were not covered with bluegreen algae or were as brittle as in October. This indicated that mats and changes in rhodolith integrity are a temporal phenomena.

The turning and movement experiments indicated that rhodolith movement was highly dependent upon local wind patterns and resulting short-period swell, which vary with season in the gulf. Wind patterns in the gulf and my observations indicated frequency of turning is greater from November to May (Alvarez-Borrego 1983). The upper portions of rhodolith beds are more dynamic than the lower but turning can occur throughout the entire bed during times of high winds. During such times movement decreases with depth.

Complete or partial restriction of movement indicated that thalli are fouled if they do not move but that limited rolling or movement (under nets) was sufficient to prevent fouling even when the overlying nets were fouled. Rolling did occur between observations, as indicated by rhodoliths on top of nets. Increased fouling of rhodoliths on stakes may have

resulted from exposure conditions 20 cm off of the bottom. Decreased fouling with depth may reflect the effect of decreased light and increased sedimentation.

Coralline growth rates vary with species, depth, light, and temperature (Adey 1966, 1970, Adey and MacIntyre 1973). A growth rate of 0.93 mm/month is a rough estimate due to low sample size and measuring growth in only two planes (X and Y) of the rhodolith. Adey and McKibben (1970) found that protuberances or branch tips of free-living corallines grow fastest in length, and for boreal species growth rates were greatest in summer. Estimating overall growth rates using branch tips may depend on branch density, and may be highly variable with species, form, and environmental conditions.

Reports of conceptacle development on unattached corallines are rare (Johansen 1981), but individuals with reproductive structures were found during my sampling in 1990-1991. Although it was not determined if conceptacles were fertile, their abundance was different from Cabioch's (1969) finding that sexual conceptacles may only occur every 4-6 years in France. The concentration of conceptacles on rhodolith branch tips in Bahía Concepción was similar to that reported by Steneck and Adey (1976). They suggested that this may increase spore dissemination. Although conceptacles were present, the primary mode of reproduction is probably fragmentation. Woelkerling (1988) suggested that although settlement may begin the process of rhodolith formation, the formation of extensive rhodoliths beds probably results from subsequent fragmentation and vegetative growth.

As a result of their variable growth forms and fossilization, the use of free-living coralline algae as paleoindicators has been suggested (Bosellini and Ginsburg 1971, Wray 1971, Toomey 1975, Steneck and Adey 1976, Minoura and Nakamori 1982, Bosence 1983b, 1985, Scoffin et al. 1985, Freiwald et al. 1991). These researchers suggested the shape, form (e.g. branching), biotic composition, and diagenic alteration can provide a sensitive record of water depth, prevailing hydraulic energy, geographic distribution, and temperature. When laminar species grow on underlying crusts, thin sections through the

individual can show changes in history in the concentric structure and taxonomic composition around a central core (Bosellini and Ginsburg 1971, Bosence 1983b). Laminar forms may contain a long, internal history of changes. Some laminar forms, with living external layers, were 100 to 10,000 years old (Bosence 1983a). Freiwald et al. (1991) compared present day rhodolith and maerl beds and nearby fossilized beds in Norwegian fjords, and suggested the conditions supporting free-living beds were geologically short-lived because specific conditions only occur during times of reduced shore level displacement. The specific conditions included lack of terrigenous dilution, shifting medium currents forced by tides not open ocean waves, and flat bottoms protected from open ocean waves. These conditions are similar to some important factors suggested in this study, indicating a better understanding of modern rhodolith beds will enhance the interpretation of environmental conditions of fossilized beds.

In a re-evaluation of deep sea (30-60 m) coralline nodules proposed for use as indicators of paleoenvironments, Reid and MacIntyre (1988) suggested that nodule shape and coralline-algal form have little predictable relationship with specific environmental conditions in the eastern Caribbean. Adey and MacIntyre (1973) warned against the interpretation of paleoenvironments based only on the presence of corallines due to misconceptions about habitats in which they grow. They concluded that rhodolith morphology, in particular, should not be related to water motion, except that massive nodules probably characterize higher energy situations than open branched forms. Species have surficial morphological differences due to light, temperature, and water motion. My data indicated that larger size and greater branch density also may be a indicator of high exposure. Though specific depth related interpretations may not be credible, the morphology of present day rhodoliths in Bahía Concepción exhibit a close relationships to hydraulic energy along horizontal and vertical gradients nearshore. If preserved as fossils, rhodolith form may be of some interpretive use.

In this study, the aerial survey was a successful method to detect the geographic distribution of rhodolith beds in Bahía Concepción. When combined with SCUBA verification, it can be used to determine the large scale geographic distribution of shallow water rhodolith beds in the Gulf of California. Depth stratified sampling of rhodoliths within beds clearly revealed depth related trends in morphology. Experimental examination of factors affecting the limits of other beds, especially those that did not follow the general trends in morphology with depth, may determine the importance of water motion and sedimentation in determining the upper and lower limits of beds as well as their geographic distribution.

Chapter 2

Organisms associated with rhodoliths in Bahía Concepción

Introduction

Diverse invertebrate and algal assemblages grow on and between the branches and protuberances of free-living coralline algae or rhodoliths of the genera *Lithothamnium* and *Lithophyllum* (Weber-van Bosse and Foslie 1904, Cabioch 1969, Bosence 1979). Similar to assemblages of organisms living in complex biotic structures of kelp holdfasts (Ghelardi 1960), mussel beds (Suchanek 1979), and coralline mats (Dearn 1987), the variable but persistent assemblages associated with free-living corallines may depend upon the structure and survival of the "substrate." The unattached coralline system is unique because the substrate can be highly mobile. The study of Hily et al. (1992) is the only work since Cabioch (1969) on the ecology of macrophytes associated with free-living shallow water (<40 m) coralline aggregations. Associated fauna were described by Cabioch (1968), Keegan (1974), and Bosence (1979) but, with the exception of Cabioch (1969) and Hily et al. (1992), most of these descriptions typically were during one sampling date so temporal changes were undescribed. The ecology of these assemblages has received little attention. Improved quantitative sampling has provided insight into among site variation (Hily et al. 1992) and differences among assemblage types (Keegan 1974, Bosence 1979). Mechanisms responsible for patterns of abundance, however, have only been suggested.

In descriptions of associated assemblages, the coralline thalli can be defined at three different scales: as the dominant algae occupying most of the primary space on a sandy/muddy bottom, as substrate for a secondary cover of algae or invertebrates, and a structure with complex internal spaces that provides additional habitat for cryptofauna. It is therefore imperative, to clearly define at which scale the community is described. Branching corallines are favorable supports for sessile fauna, and provide refuge for epibenthic vagile species, especially juveniles (Hily 1989). Bosence (1979) divided organisms associated with coralline beds into ecological groups including vagile and sessile epifauna, and boring, deposit and suspension feeding infauna.

A number of abiotic and biotic factors may influence the distribution of canopy organisms associated with unattached corallines. Cabioch (1969) suggested that the distribution and temporal variation of macrophytes associated with maerl (rhodolith) beds along the temperate Brittany coast in France may be influenced by the seasonal extension of oceanic waters and differences in coastal hydrodynamics. Warm temperature flora persisted in areas adjacent to streams because streams stabilized environments by distributing warm summer waters deeper. In a recent study in the Bay of Brest, also on the Brittany coast, Hily et al. (1992) encountered vastly different floral assemblages than Cabioch (1969), and attributed these differences to changes in coastal turbidity, not temperature or salinity. Hily et al. (1992) also reported that small-scale variations in plant distribution were due to differences in hydrodynamic disturbance and sedimentation. Both studies were entirely descriptive, making it difficult to resolve the causality of distributional patterns without further research. Jacquotte (1962) and Keegan (1974) indicated plant and animal assemblages in temperate maerl beds varied with type of maerl (littoral or superlittoral, dead or living) and associated substrate. Differences in associated assemblages also have been attributed to bathymetry as it affects light (Freiwald et al. 1991). Hily et al. (1992) suggested that biotic factors such as interspecific competition for space and herbivory may affect associated algal assemblages.

Dawson (1960) described free-living coralline beds of *Lithothamnium australe* in Panama, which covered the bottom to the near exclusion of all other organisms. He apparently was not referring to infaunal invertebrates. A rich invertebrate assemblage occurs in the structure of these branching algae (Steneck 1986), and infaunal distribution is related to habitat complexity. Weber-van Bosse and Foslie (1904) observed that branching corallines (*Lithothamnia*) in the South Pacific provided shelter for animals adapted in form and color for living in the branches. Sparsely branched forms had fewer animals (gastropods, worms, and ophiuroids), and Weber-van Bosse and Foslie (1904) speculated that this was due to the poor shelter provided. Habitat heterogeneity or structural

complexity have been considered a physical feature that directly or indirectly affect species diversity and abundance (Pianka 1966, Pielou 1975). By increasing three-dimensional space, more branches create a more complex habitat, which can support more individuals. Although this pattern of organism abundance has been observed in rhodoliths, it has not been quantified.

The objectives of this study were to describe the abundance and distribution with depth and time of the epifloral, epifaunal, and cryptofaunal organisms associated with a rhodolith bed in Bahía Concepción, Baja California Sur, México. No prior studies have been conducted in this region on the organisms directly associated with these free-living corallines. The questions investigated in this study included: what secondary canopy and infaunal organisms are present in rhodolith beds, and does their distribution along a depth gradient vary in time? What is the relationship between spatial complexity of rhodolith thalli and the taxonomic composition of infaunal invertebrates? Do cryptofaunal assemblages in rhodoliths differ from the infauna in the substrate below, and does structure or living substrate influence species colonization?

Methods and Materials

Epiflora and epifauna

The abundance and distribution of epiflora and epifauna associated with the rhodolith bed at Isla El Requesón were estimated using depth stratified random sampling at the three sites described in Chapter 1 plus at a fourth site located approximately 300 m south of site 3 (Fig. 4). Sampling dates and sites were: April 1990 - sites 1, 2, and 3, January 1991 - sites 1, 2, 3, and 4, and June and October, 1991 - sites 1, 2, and 4. At each site, 20 m long transects were placed parallel to shore 5 m below the upper edge (5 m depth), in the middle of the bed (8 m depth), and 5 m above the lower edge (12 m depth). Organisms were sampled in four 1 m^2 quadrats randomly placed along each transect line. Motile animals (bivalves, urchins, and sacoglossans) were counted. Percent cover of sessile organisms (foliose algae, bluegreen algae/diatom mats, tunicate/sponge mats, anemones, and the bivalve *Pinna rugosa*) was estimated from 10 random points/quadrat using a point quadrat (Cowen et al. 1982). In April 1990 percent cover was visually estimated. Anemones were counted in a 0.25 m^2 quadrat within the 1m^2 quadrat in April 1990 and October 1991, and their cover estimated with point quadrats in four 0.25 m^2 quadrats in January, June, and October, 1991.

All invertebrates and algae were identified to species or genera when possible. Some invertebrate identifications were done using Brusca (1973) and the Gulf of California reference collections at the California Academy of Sciences. Anemones were identified with the help of D. Fautin (Univ. of Kansas), and sponges by K. White using reference material from Dickenson (1954). A free-living coral was identified by P. Glynn (Univ. of Miami), and algae were identified in collaboration with J. Norris (Smithsonian) and W. Woelkerling (La Trobe Univ.). A new species of chiton was determined by B. Putnam (Cuesta College), and some crustacean and polychaete identifications were done with the help of P. Slattery and J. Oliver (Moss Landing Marine Laboratories).

Size frequencies of the sea urchin Arbacia incisa at site 1 were estimated at four depths in June 1991, when their abundance was very high. The depths included the three described above (5, 8, and 12 m) and beyond the lower margin of the bed in silty sediment (13.8 m depth). Test diameter (cm) was determined for 20 urchins collected at random locations along 20 m transects at each depth.

Infauna

The invertebrate cryptofauna in rhodoliths were sampled in individual rhodoliths collected at 5, 8, and 12 m depths from sites 1 and 4 at Isla El Requesón in June 1991. The largest rhodolith was collected within 10 cm of 10 random points along a 20 m transect at each depth. Whole rhodoliths were individually preserved in 5% formalin, and then transferred to 70% ethanol for storage. Spacial complexity of each rhodolith was estimated by measuring branch density (# branches/cm^2). This was done by counting the apical tips of all branches in five one cm^2 quadrats haphazardly placed on the thallus surface of each plant. Size (longest dimension in cm.) and wet weight of plants also were measured. If thalli were broken, morphological data were not included in the analysis.

All macro and micro invertebrates visible under a 40x dissecting scope were removed from the thalli, sorted by taxa, counted, and identified to species when possible. To test whether mean branch density or number of invertebrates/rhodolith differed among sites and depths a Model 1 two-factor (site and depth) ANOVA was used. Before analysis, data sets were examined for normality and homogeneity of variances using Cochran's test (Winer 1971). Log transformations were used where necessary. A Scheffé *a posteriori* multiple comparison test was used when appropriate. Correlations were used to compare the relationship between total number of cryptofauna/rhodolith and branch density for each depth.

Cryptofaunal assemblages in rhodoliths and the infauna in underlying sediment were sampled in October 1991 and compared to examine the relationship between organism abundance and structural complexity of the substrate. Four cylindrical cores,

approximately the same volume as rhodoliths (6 cm length x 5.5 cm diameter - or 40 cm^3), were randomly taken in the sediment underlying rhodoliths at random points along transects at 5, 8, and 12 m depths at site 1. A rhodolith next to each core was collected for comparison. The core material was sieved through a 0.50 mm mesh screen and, like the rhodoliths, the organisms retained on the screen were individually preserved in 5% formalin and then transferred to 70% ethanol. Infaunal organisms were removed, sorted by taxa, identified to species if possible, and counted. A two-factor ANOVA was used to test whether mean infaunal/cryptofaunal abundance was different between depths and substrate types.

A four-day colonization experiment was conducted in October 1991 to determine if organisms would occupy artificial rhodoliths. Plastic, hollow, perforated golf balls, approximately the size of rhodoliths (6 cm diameter), were filled with either rhodolith fragments devoid of organisms or non toxic polycarbonate shavings whose rigid structure simulated rhodolith branches. Six balls of each treatment were placed at 5 m depth in the rhodolith bed. These, along with six rhodoliths from the same depth used as controls for the organisms available for colonization, were collected after four days. Samples were treated as for cryptofauna above.

Results

Foliose algae covered approximately <15% of the bottom at all sampling dates, growing over the coralline thalli and on shells of the large bivalve pen shell *Pinna rugosa* (Fig 12). Common rhodophytes included *Polysiphonia* spp. and *Amphiora* spp. and common phaeophytes included *Dictyota cf. divaricata*, and *Rosenvingea intricata* (Appendix I). The slightly calcified brown alga *Padina durvillaei* occasionally overgrew entire rhodoliths but this plant was patchy in distribution. *Sargassum sincola* and *Sargassum herporhizum* were abundant in the rocky subtidal above the rhodolith bed, and the annual reproductive fronds formed thick canopies nearshore in April 1990 and June 1991. When *Sargassum* spp. were present in the bed it grew on partially buried valves of living pen shells, not on rhodoliths. Nodular, nongeniculate corallines also encrusted pen shells. In October 1991, when water temperature was high and most organisms were rare, bluegreen algal/diatom mats had the highest cover of any sampling period (Fig 12). These mats were not apparent during any other sampling period.

Tunicates (*Polyclinum laxum, Aplidium* sp.) and sponges (*Lucetta* cf. *losangelensis, Tendania* sp., *Mycale* sp., Appendix I) generally grew as small clumps (~ 10 cm^2) or large, ephemeral mats (> 0.25m^2) over rhodoliths. Tunicates and sponges were considered as one category because they often co-occurred in the same mat and were sometimes difficult to differentiate in the field (Fig. 12). They were always present, and usually more abundant in the middle. Overall abundance declined from January to October.

The bivalves *Argopectin circularis, Chione* spp., *Glycimeras gigantea, Tivela planulata* (Appendix I) were always present and generally more abundant in the middle and lower rhodolith bed (Fig. 12). The swimming scallop, *A. circularis*, was the most abundant bivalve in middle and lower regions, lying on the surface of rhodoliths. *Chione* spp. were more common in shallow regions, partially buried in sediment between

rhodoliths. A large decrease in abundance, mainly in populations of *A. circularis*, occurred at the lower transects in October 1991.

The pen shell P. rugosa grows to 20 cm (Brusca 1983), and were often buried up to 15 cm in rhodolith substrate. They were commonly used as substrate by foliose algae and sessile organisms not generally found on rhodoliths. Patches of the bivalve *Arca pacifica* often covered the valves. Pen shells were rare and patchy, and occurred primarily at middle depths (Table 9).

The most common urchin was *Arbacia incisa.* Only two slate pencil urchins *Eucidaris thouarsii,* were counted, and the flower sea urchin, *Toxopneustes roseus,* was observed occasionally but only at night and therefore not sampled. Sea urchin abundance was generally low but variable. They were most abundant in June 1991 near the lower edge of the rhodolith bed (Fig. 13). Urchin numbers decreased rapidly on the muddy sediment below ($x \pm$ S.E. = $100.9/m^2 \pm 15.5$) at the lower transect to $9.75 \pm 10.5/m^2$ beyond the lower margin). Sea urchins test size was significantly different (ANOVA $p=0.002$) and individuals were slightly larger at mid-depths (Table 10). An apparent die off occurred after June as indicated by low abundance and the high numbers of spines and empty tests in October 1991.

Small anemones (*Diadumene lineata, Haplanella luciae*) living in the branched thalli generally were most abundant in the middle of the rhodolith bed (Table 9). Similar abundance patterns were detected in October 1991 when both methods for estimating abundance were used. Anemones grew in close association with bluegreen algal/diatom mats in October 1991, and were one of the few organisms that did not decrease in abundance at this time.

Tridachiella diomedea was a common sacoglossum, and was first found in January 1991. It was abundant at middle depths associated with foliose algae, sponges, and

tunicates (Table 9). None were found in October 1991 when most associated organisms were gone.

Other conspicuous organisms were present in other beds in the bay and were collected for identification. Coralliths, free-living forms of the coral *Porites californica*, were found living among rhodoliths especially at beds 1 and 6 (Chapt. 1, Fig. 1). Two forms were present; one encrusting a core of foreign material and the other composed almost entirely of complex branches to 10 cm in length and 1.5 cm in diameter. Sizes ranged from 3.0 to 25.0 cm in diameter. Individual gorgonian colonies (*Muricea californica*) infrequently occurred attached to rhodoliths.

Cryptofauna

Many cryptofauna were found living in rhodoliths (Appendix II). Number of invertebrates/rhodolith and branch density/rhodolith decreased with increased depth at sites 1 and 4 (Fig. 14, Table 11). There were no statistically significant interactions between site and depth and no significant correlations between branch density and number of individuals at any depth (r^2 0.188 (5 m depth), 0.023 (8 m), and 0.477 (12 m).

There were more cryptofauna in rhodoliths than sediments at upper transects; however, the opposite occurred at lower depths (Table 12). A significant interaction between substrate and depth indicated the effect of substrate type on total individuals changed with depth (Table 13); more cryptofauna occurred in rhodoliths in upper and middle depths but fewer (relative to sediment) in lower transects. By separating taxa into groups some substrate related trends were apparent (Table 12). In general there were more ophiuroids, anemones, and chitons in rhodoliths and more polychaetes, crustaceans, and molluscs (not including chitons) in the sediments. The ophiuroids and anemones, common in rhodoliths, decreased with depth and few were present in the sediment. Small (<1 cm) chitons (*Acanthochiton avicula, Ischnochiton cyanomaculatus*) were found on rhodolith branches primarily at upper and middle depths but were rare or absent in

rhodoliths from lower transects and in sediments. Polychaetes in rhodoliths decreased with increasing depth. They were more abundant in the sediments in the middle of the bed. A boring clam, *Lithophaga aristata*, was common at the center of densely branched rhodoliths.

Colonization of experimental treatments occurred within four days (Fig. 15). Polycarbonate shavings and rhodolith fragments had similar number of infauna. All colonizing taxa were present in natural rhodoliths, but more gastropods were found in experimental treatments and there was a greater number of crustaceans in rhodolith fragments. Overall, there were more individuals in natural rhodoliths, particularly ophiuroids (*Ophiothrix spiculata* and *Ophiactis savignyi*), than experimental treatments.

Discussion

The most apparent patterns from the four sampling periods were high temporal variation and distinct depth distribution of plants and animals associated with the rhodolith bed at Isla El Requesón. The decline of most organisms and increase in bluegreen algae and diatom mats corresponded with an increase in seasonal water temperatures and salinities (Chapt. 1, Alvarez-Borrego 1983, Maluf 1983), a decrease in particulate organic matter (Martinez-Lopez et al. 1992), and a decrease in strong northerly winds (Candella et al. 1984a, b, Merrifield et al. 1987) in Bahía Concepción. This temporal variation may not be as apparent in more temperate rhodolith beds (Cabioch 1969, Hily et al. 1992) where abiotic factors may not be as variable.

Organisms living in shallow water may be more affected by water motion and temperature changes whereas others, such as filter feeders, may be more susceptible to sedimentation in deeper water. High disturbance of coralline covered cobbles by water motion can greatly decrease the amount of algae on cobble surfaces (Lieberman et al. 1979). The concentration of most organisms in the middle and lower portions of the bed may be in response to the decreased rolling of rhodoliths at these depths (Chapt. 1). Sessile sponge and tunicate mats and foliose algae may not survive high disturbance, and their distribution may reflect adaptations to this highly variable environment. But disturbance from water motion varies temporally, and its effect on the community of organisms is confounded by changes in temperature, salinity, light, and nutrients. During times of greater water motion in April 1990 and January 1991, organisms were diverse but low in abundance. In October 1991, when water motion was reduced, abundance was highest but diversity was low, cover was primarily bluegreen algae and diatoms. Temperature, salinity, and light may be more important on a temporal scale, and variation in water motion more influential on a spatial (depth related) scale. Although these data were collected at only one bed, similar patterns including bluegreen algal/diatom blooms were observed at other beds in the bay.

The abundance and distribution of most organisms appeared related primarily to the influence of abiotic factors and the biology of the organisms. Partial burial in the substrate at shallow regions of the bed may enable the bivalve *Chione* spp. to live among the dynamic rhodoliths, whereas the surface dwelling *A. circularis* may avoid disturbance by living deeper and avoiding sedimentation by being motile. The decrease in bivalve abundance from June to October 1991 at the lower bed region may have been associated with the annual commercial harvest of *A. circularis* by local fishermen. Harvest in the bed around Isla El Requesón was observed in June after sampling had occurred. Concentrations of *P. rugosa* in the middle of the bed may also reflect an intermediate distribution of these filter feeders between extremes of water motion and sedimentation. Temporal changes in the abundance of sea urchins and sacoglossans may reflect changes in food sources, reproductive cycles, or an intolerance of high water temperatures.

The sphericity of free-living *Porites californica* coralliths indicated they overturn like rhodoliths. This may not occur as often in larger individuals (~25 cm) as suggested by dead areas on the portion of large individuals touching the substratum. Glynn (1974) suggested that coralliths in the Gulf of Panama were overturned by frequent disturbance of bottom sediments, principally from browsing fish. Disturbance by water motion seems to be the primary factor influencing overturning coralliths in Bahía Concepción.

The high density of organisms colonizing highly branched rhodoliths is similar to observations by others (Weber-van Bosse and Foslie 1904, Bosence 1979, Keegan 1974, Steneck 1986), and the density of infaunal organisms may be dependent upon structural complexity. Branch density and cryptofaunal abundance, however, declined with increasing depth, suggesting that some other factor associated with depth may affect infaunal abundance. Structural complexity or more highly branched forms are generally found at shallower depths. This variation in branch density or spacial complexity has been related to degree of water motion at other locations (Wray 1977, Bosence 1976) and also may be influenced by light and sedimentation.

To examine the influence of spatial complexity on cryptofaunal densities without a depth effect, rhodoliths with a wide range of branch densities should be examined at one depth. This is difficult as branch density in Bahía Concepción is generally depth dependent (Fig. 6, 7, 13). However, at Isla El Requesón spatial complexity varied on a horizontal scale, where branch density and total individuals/rhodolith differed among sites at similar depths (Fig. 13). The lower abundance of individuals corresponded with lower branch densities, suggesting cryptofaunal abundance was directly related to spatial complexity regardless of depth.

The overall shift in infaunal abundance from rhodoliths to sediment with increased depth (Table 12) further indicated that the presence of some cryptofauna in rhodoliths is dependent upon spatial complexity. This shift may be affected by change in biology of the organisms. Ophiuroids, chitons, and anemones, generally uncommon in sediments, were more common in densely branched thalli, and may require a complex habitat for filter feeding, grazing, and shelter. The shift of polychaetes from rhodoliths to sediments with increased depth may result from their adaptability to living in variable environments. It also may reflect a change in polychaete species composition.

Invertebrates colonized artificial substrates and appeared to show no preference between rhodolith fragments and polycarbonate shavings. This again indicated spatial complexity was an important feature in highly colonized substrates. These results are similar to Dearn (1987), who found invertebrates inhabited articulated coralline mats primarily in response to the physical structure of the mats. A unique difference between kelp holdfasts, mussel beds, and coralline mats is that rhodoliths are more mobile. Ultimately, the abundance of cryptofauna in rhodoliths appears dependent upon substrate mobility, as increased turning results in higher branch density and more organisms colonizing areas of higher spatial complexity.

Although this study was limited to one location, the temporal, depth-stratified sampling using SCUBA, allowed detection of patterns that would have been missed by sampling at

one time with a trawl or dredge. There was apparently some human disturbance due to the commercial harvest of scallops but this probably did not affect the abundance of other organisms. Patterns of abundance varied with time, depth, and spatial complexity of rhodoliths. These results indicated the importance of sampling through time at different spatial scales when characterizing the plant and animal communities associated with unattached corallines. Detecting temporal patterns is essential to the design of realistic experiments that examine causes of patterns.

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Table 1. Environmental data collected at Isla El Requesón, Bahía Concepción. N.D. = no data.

Date	Water Temperature (°C)	Salinity (o/oo)	Secchi Depth (m)
April, 1990	22.2	35.0	6.0
January, 1991	18.5	N.D.	6.5
June, 1991	26.0	36.5	6.7
October, 1991	29.5	36.0	9.1

Table 2. Results of a 2-way ANOVA testing the effects of different beds and transect depths on longest dimension, branch density, and wet weight for rhodoliths collected at nine beds in Bahía Concepción. Branch density and wet weight data were log transformed, n = 270.

Longest Dimension (X)

SOURCE:	DF	SS	MS	F	P
BED(A)	8	106.81	13.352	31.59	< 0.001
DEPTH(B)	2	13.53	6.762	16.14	< 0.001
AxB	16	83.15	5.197	12.29	< 0.001
ERROR	243	102.71	0.423		

Branch Density (BD)

SOURCE:	DF	SS	MS	F	P
BED(A)	8	3.86	0.482	33.64	< 0.001
DEPTH(B)	2	4.28	2.14	149.18	< 0.001
AxB	16	3.05	0.19	13.31	< 0.001
ERROR	243	3.49	0.014		

Wet Weight (WW)

SOURCE:	DF	SS	MS	F	P
BED(A)	8	3.86	3.093	69.01	< 0.001
DEPTH(B)	2	4.28	4.407	98.35	< 0.001
AxB	16	3.05	0.702	15.67	< 0.001
ERROR	243	3.49	0.045		

Table 3. Proportion of rhodoliths in each branching class based on Bosence (1976) by transect depth (U=upper, M=middle, L=lower, depths indicated on Fig. 5). Plants collected at three transect depths at nine sites in Bahía Concepción (n=10, except * n=7, - = no data).

Bed	1			2			3			4			5		
	U	M	L	U	M	L	U	M	L	U	M	L	U	M	L
III	-	-	-	-	0.1	0.7	-	1.0	0.9	0.3	- *	0.6	-	-	0.6
IV	1.0	1.0	1.0	1.0	0.9	0.3	1.0	-	0.1	0.7	0.7	0.4	0.1	0.1	0.4

Bed	6			7			8			9		
Class	U	M	L	U	M	L	U	M	L	U	M	L
III	-	0.2	0.9	0.1	-	0.7	-	-	-	1.0	-	0.2
IV	1.0	0.8	0.1	0.9	1.0	0.3	1.0	1.0	1.0	-	1.0	0.8

Table 4. Two-way ANOVA results from multi-site sampling in one bed at Isla El Requéson, April 1990. Underlining designates similarities between sites and depths designated by Scheffé multiple comparison tests on significant factors. Wet weight data were log(x) transformed, n = 4.

Longest Dimension (X)

SOURCE:	DF	SS	MS	F	P			
SITE(A)	2	0.566	0.283	2.455	0.1048			
TRANSECT DEPTH(B)	2	1.903	0.951	8.25	0.0016	U	M	L
AxB	4	0.851	0.212	1.843	0.1498			
ERROR	27	3.114	0.115					

Branch Density (BD)

SOURCE:	DF	SS	MS	F	P			
SITE(A)	2	86.17	43.083	19.832	<0.001	1	2	3
TRANSECT DEPTH(B)	2	158.15	79.076	36.4	<0.001	U	M	L
AxB	4	17.57	4.393	2.022	0.1196			
ERROR	27	58.66	2.172					

Wet Weight (WW)

SOURCE:	DF	SS	MS	F	P			
SITE(A)	2	0.533	0.267	5.42	0.0105	1	2	3
TRANSECT DEPTH(B)	2	3.12	1.56	31.702	<0.001	U	M	L
AxB	4	0.294	0.073	1.493	0.232			
ERROR	27	1.329	0.049					

Table 5. Proportion of rhodoliths in each branching class at Isla El Requesón (based on classes of Bosence 1976). Plants collected from cores at three transect depths (U=upper, 4-5 m, M=middle, 6-8 m, L=lower, 8-10 m) at three sites around Isla El Requesón, April 1990.

	Site								
	1			2			3		
	Depth			Depth			Depth		
Class	U	M	L	U	M	L	U	M	L
II	-	-	0.15	-	0.13	0.03	0.03	0.05	0.05
III	0.20	0.18	0.63	0.03	0.25	0.67	0.07	0.63	0.60
IV	0.80	0.82	0.22	0.97	0.62	0.30	0.90	0.32	0.35
n =	30	34	40	40	40	30	40	40	40

Table 6. Mean distance (cm) of rhodolith movement away from a stake at four different depths in the rhodolith bed at Isla El Requesón at three different sampling times (T1=1 day, T2=2.5 days, T3=5 days).

Depth	T1 (1 day)		T2 (2.5 days)		T3 (5 days)	
m	$\bar{x}$	n	$\bar{x}$ S.E.	n	$\bar{x}$ S.E.	n
3	0	10	69.0 ± 29.2	7	90.0 ± 30.1	6
5	0	10	3.9 ± 1.5	10	6.4 ± 2.5	10
7	0	10	0.8 ± 0.8	10	7.0 ± 3.3	10
11	0	10	0.5 ± 0.5	10	3.1 ± 1.0	10

Table 7. Mean percent cover of rhodoliths in netted and control (1m2) plots during three different sampling dates (n=3). There was no significant difference between netted and control areas using two-tailed unpaired t-tests for any sampling date.

	Netted		Control	
	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.
January	90.0	± 2.9	88.0	± 1.7
June	91.7	± 1.7	85.0	± 5.0
October	88.3	± 7.26	73.3	± 8.8

Table 8. Total percent cover of all fouling organisms on staked rhodoliths and controls for the two sampling dates at three depths and results of a two-way ANOVA done on October 1991 arcsine transformed data.

Percent cover

	Sampling date 1991					
Treatments by depth	June			October		
Staked rhodoliths	$\bar{x}$ ±	S.E.	n	$\bar{x}$ ±	S.E.	n
upper	42.5 ±	17.9	4	70.0 ±	23.8	4
middle	52.5 ±	20.6	4	100.0 ±	0.0	4
lower	0.0 ±	0.0	2	50.0 ±	35.4	2
Controls						
upper	2.5 ±	2.5	4	42.5 ±	7.5	4
middle	10.0 ±	4.1	4	55.0 ±	2.9	4
lower	0.0 ±	0.0	4	42.5 ±	7.5	4

ANOVA - October 1991

SOURCE:	DF	SS	MS	F	P
Treatment (A)	1	2.069	2.069	10.794	0.0047
Depth (B)	2	0.816	0.408	2.128	0.1516
AxB	2	0.364	0.182	0.949	0.4079
Error	16	3.067	0.192		

Table 9. Mean number± S.E. of Pinna rugosa, Tridachiella diomedea, and anemones (Diadumene lineata, Haplanella luciae) by depth and sampling date, - = not sampled.

Date	Position	Depth (m)	n	Pinna rugosa/m2 ($\bar{x}$ ± S.E.)	Sacoglossans/m2 ($\bar{x}$ ± S.E.)	Anemones/m2 ($\bar{x}$ ± S.E.)	% cover Anemones ($\bar{x}$ ± S.E.)
Apr-90	Upper	4.6-5.2	12	0.1 ± 0.1	-	594.7 ± 320.0	-
	Middle	6.4-7.9	12	0.8 ± 0.4	-	250.3 ± 51.0	-
	Lower	7.6-11.9	12	0.3 ± 0.1	-	53.0 ± 18.1	-
Jan-91	Upper	3.9-5.8	16	0.2 ± 0.1	0.3 ± 0.2	-	12.5 ± 2.8
	Middle	7.6	16	1.6 ± 0.5	0.7 ± 0.3	-	20.0 ± 4.8
	Lower	12.2	16	0.1 ± 0.1	0.3 ± 0.2	-	2.5 ± 1.7
Jun-91	Upper	3.9-4.6	12	0.1 ± 0.1	0.0 ± 0.0	-	0.0 ± 0.0
	Middle	6.4-7.9	12	3.5 ± 0.5	1.3 ± 0.6	-	9.2 ± 3.6
	Lower	10.1-11.6	12	0.0 ± 0.0	0.8 ± 0.8	-	5.8 ± 3.6
Oct-91	Upper	3.9	12	0.0 ± 0.0	0	177.0 ± 38.1	3.3 ± 1.9
	Middle	7.6	12	1.1 ± 0.6	0	511.7 ± 50.4	13.3 ± 3.3
	Lower	10.7-12.2	12	0.1 ± 0.1	0	126.0 ± 35.4	4.2 ± 2.3

Table 10. Mean ± S.E. Arbacia incisa test diameters (cm) for individuals collected at threee depths in the rhodolith bed and one depth below. Size varied significantly with depth (ANOVA, p = 0.002).

Depth (m)	n	mean ± S.E.
4.2-5.5	20	1.2 ± 0.06
6.7-8.7	20	1.5 ± 0.07
8.06-12.9	19	1.3 ± 0.07
13.5	20	1.2 ± 0.04

Table11. Two-factor ANOVA for the effect of site (Sites 1 and 4) and depth (5, 8, 10 m) on rhodolith branch denisty and total infaunal abundance. Bold underlining signifies significant differences between factors designated by the Sheffé a posteriori test.

Variable	n	source	df	ms	F ratio	P value	one	four	
total individuals (log x+1)	9	site	1	1.872	17.2	<0.001			
		depth	2	5.049	23.196	<0.001	U	M	D
		site x depth	2	0.108	0.498	0.611			
		error	48	5.224					
branch density (log x+1)	8	site	1	0.14	15.56	<0.001			
		depth	2	0.819	45.49	<0.001	U	M	D
		site x depth	2	0.029	1.62	0.24			
		error	42	0.378					

Table 12. Mean (x) number of cryptofaunal and infaunal taxa (± S.E.) in rhodoliths and sediment at three depths.

Taxa	Habitat	Upper (5 m) ($\bar{x}$ ± S.E.)	Middle (8 m ($\bar{x}$ ± S.E.)	Lower (12 m) ($\bar{x}$ ± S.E.)
total individuals	rhodolith	67.5 ± 16.2	32.5 ± 7.8	7.3 ± 2.5
	sediment	11.0 ± 2.1	23.3 ± 6.6	11.8 ± 1.8
ophiuroids	rhodolith	31.5 ± 13.2	12.8 ± 3.1	2.0 ± 1.4
	sediment	0.0 ± 0.0	1.3 ± 0.8	2.3 ± 1.9
polychaetes	rhodolith	18.0 ± 3.2	6.3 ± 0.5	2.3 ± 1.1
	sediment	5.8 ± 1.1	20.0 ± 7.2	6.8 ± 2.7
crustaceans	rhodolith	2.3 ± 1.0	3.3 ± 2.9	0.0 ± 0
	sediment	3.5 ± 1.2	0.5 ± 0.3	0.5 ± 0.3
chitons	rhodolith	4.0 ± 1.8	2.5 ± 1.2	0.0 ± 0
	sediment	0.0 ± 0.0	0.3 ± 0.3	0.3 ± 0.3
other molluscs	rhodolith	1.8 ± 0.9	0.3 ± 0.3	0.0 ± 0
	sediment	1.5 ± 1.2	0.3 ± 0.3	2.0 ± 1
anemones	rhodolith	8.5 ± 2.0	7.5 ± 3.0	1.5 ± 0.3
	sediment	0.3 ± 0.3	0.8 ± 0.8	0.0 ± 0

Table 13. Two-factor ANOVA for the effect of treatment (rhodoliths, sediment) on total number of individuals. Data were log (x+1) transformed.

Variable	n	source	df	ms	F ratio	P value
Total individuals log (x+1)	4	treatment	1	0.28	4.95	0.039
		depth	2	0.627	11.08	< 0.001
		treatment x depth	2	0.565	9.98	0.002
		error	18	0.057		

Figure captions

Figure 1. Bahía Concepción (enlarged) along the eastern coast of Baja California Sur, México showing location of 13 rhodolith beds (blackened) sighted in an aerial survey of the bay. Rhodoliths were sampled using SCUBA in beds 1-9.

Figure 2. Morphological variation in rhodoliths from Bahía Concepción, BCS, México. Top two rows show ranges of blunt-branched forms (fitting descriptions of *Lithothamnion australe*, and *Lithophyllum pallescens*, Dawson 1960) and the bottom row shows range of fan-branched forms (fitting descriptions of *Lithophyllum veleroae*, and *Lithophyllum diguetii*, Dawson 1960). Scale (coin) = 1.8 cm dia.

Figure 3. Sites in the rhodolith bed around Isla El Requesón where rhodoliths and associated organisms were sampled at positions of transects within sites (upper, middle, and lower).

Figure 4. Depth profile of the rhodolith bed at Isla El Requesón. *Sargassum* spp. grew seasonally (plants present in April and June) on the volcanic, rocky shore.

Figure 5. Depth (m) of upper and lower edges of all beds sampled versus the distance from the mouth of the bay (km). See Fig.1 for locations.

Figure 6. A., B., C. Morphological variation with depth ($x \pm$S.E.) in the nine beds sampled. a.) longest dimension; b.) branch density; c.) wet weight, n=10. Absolute depths in Fig 5.

Figure 7. A., B. Morphological variation with depth ($x \pm$S.E.) at three sites around Isla El Requesón. a.) longest dimension; b.) branch density; c.) wet weight; for the upper (4-5 m), middle (6-8 m), and lower (8-10 m) transect depths at sites 1, 2, and 3, n=4.

Figure 8. A., B. Size class distribution of rhodoliths and pigmented fragments $\geq$1 cm from two depths (4-5 m, and 8-10 m) at Isla El Requesón. Totals of two cores per depth from Sites 1 and 4).

Figure 9. Distribution of rhodolith sphericity at upper (4-5 m), middle (6-8 m), and lower (8-10 m) transect depths. Each point represents sphericity of one rhodolith (n=30/depth). Sphericity is plotted on the sphericity-form diagram from Sneed and Folk (1954). S, I, and L symbols stand for shortest, intermediate, and longest dimension or (X, Y, and Z in this paper). Equations are used to determine placement along respective axes.

Figure 10. A, B, C. Relationships between morphological variables of rhodoliths. Regressions of A.) longest dimension (cm) r^2=0.759, B.) branching density (#/cm^2) r^2=0.157, C.) combination of all morphological variables (volume x branch density) as a function of wet weight r^2=0.892 (n=630).

Figure 11. A., B., C. Abundance (x±S.E.) of common sessile organisms associated with the rhodolith bed at Isla El Requesón at three depths on four sampling dates. Depths: upper = 5 m, middle = 8 m, lower = 12 m. All sites combined: n=12 except January 1991 when n=16. A.) foliose algae, B.) bluegreen algal/diatom mats, C.) tunicate and sponge mats.

Figure 12. A., B. Abundance (x±S.E.) of common motile organisms associated with the rhodolith bed at Isla El Requesón at three depths on four sampling dates. Depths: upper = 5 m, middle = 8 m, lower = 12 m. All sites combined: n=12 except January 1991 when n=16. A.) bivalves, B.) urchins.

Figure 13. A, B. Branch density (#/cm^2) and the total individual taxa/rhodolith (x±S.E.) at three transect depths (5, 8, and 12 m) at two sites around Isla El Requesón, branch density n = 8, total number of individuals, n=9.

Figure 14. Total individual taxa/rhodolith and total number of individuals per group (x±S.E.) for control rhodoliths and experimental treatments: artificial (polycarbonate shavings) rhodoliths, and rhodolith fragments.

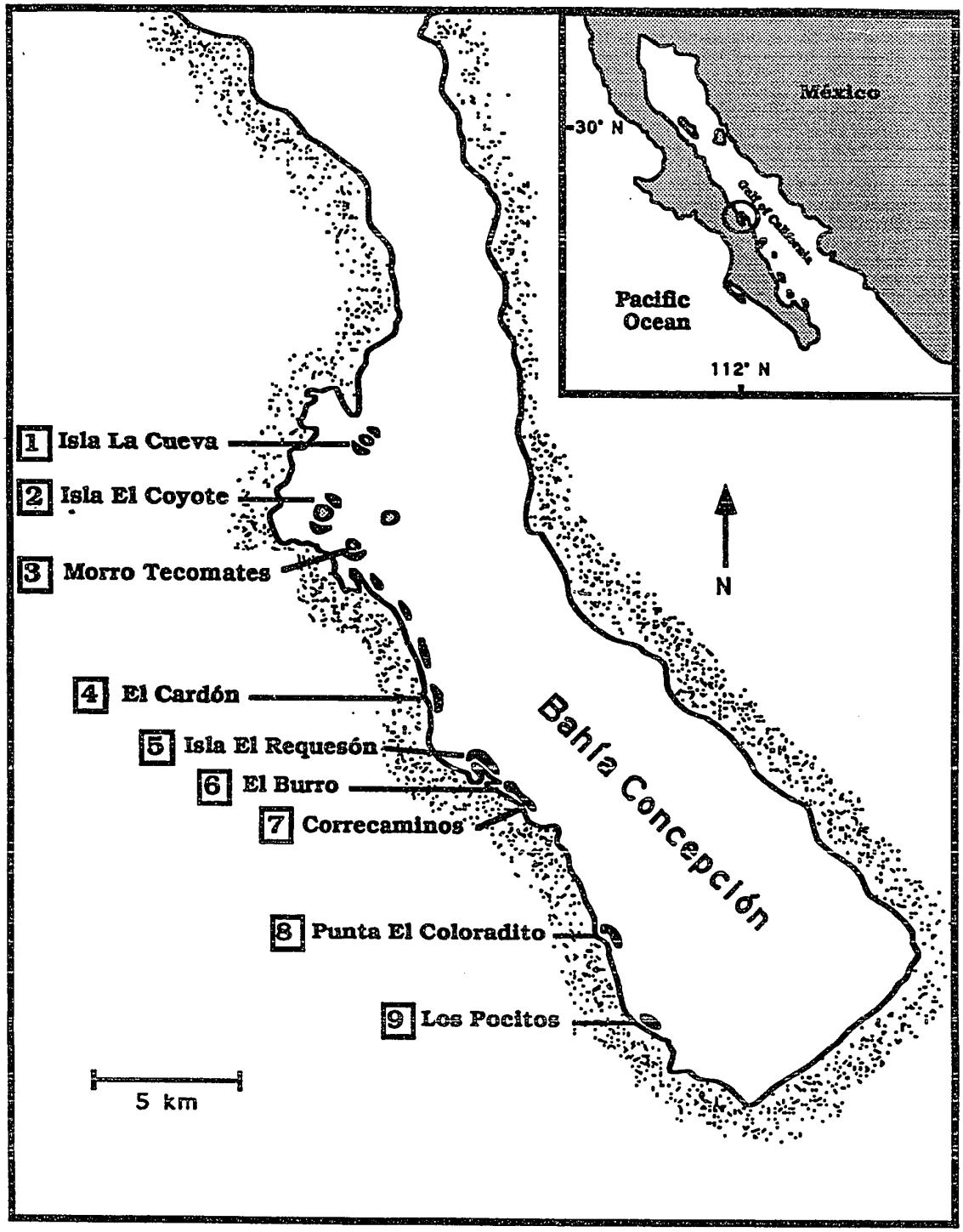

México
30° N
Gulf of California
Pacific Ocean
112° N
1 Isla La Cueva
2 Isla El Coyote
3 Morro Tecomates
4 El Cardón
5 Isla El Requesón
6 El Burro
7 Correcaminos
8 Punta El Coloradito
9 Los Pocitos
Bahía Concepción
N
5 km

Figure 1

SANTA
ROSALIA

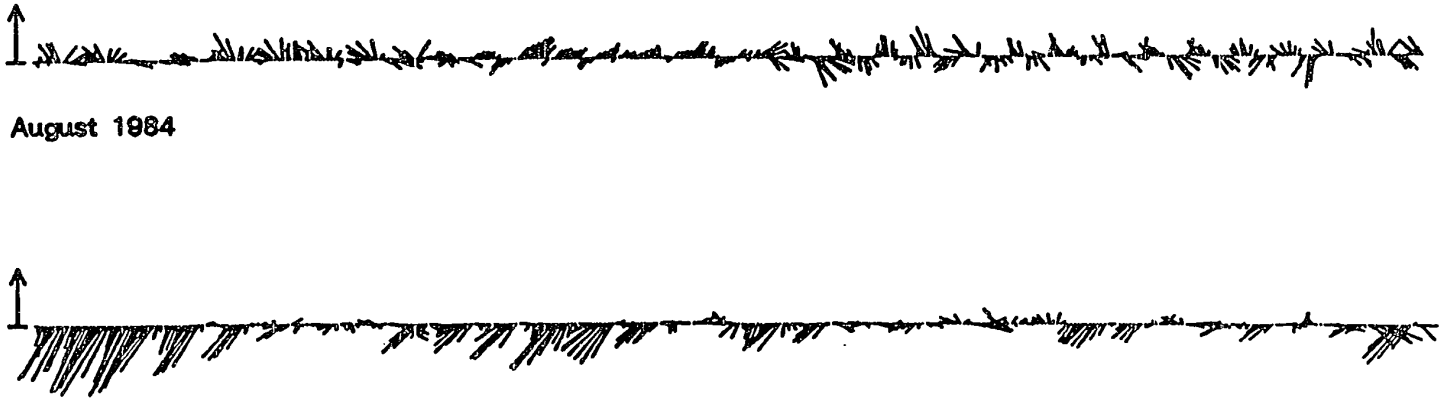


Figure 2

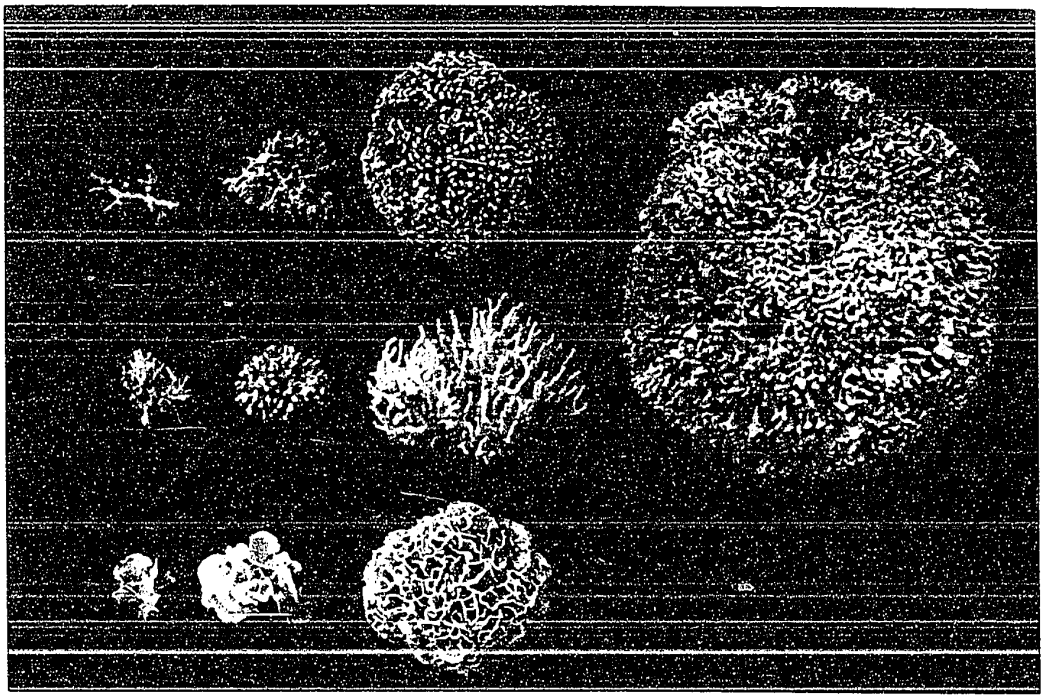


Figure 3.

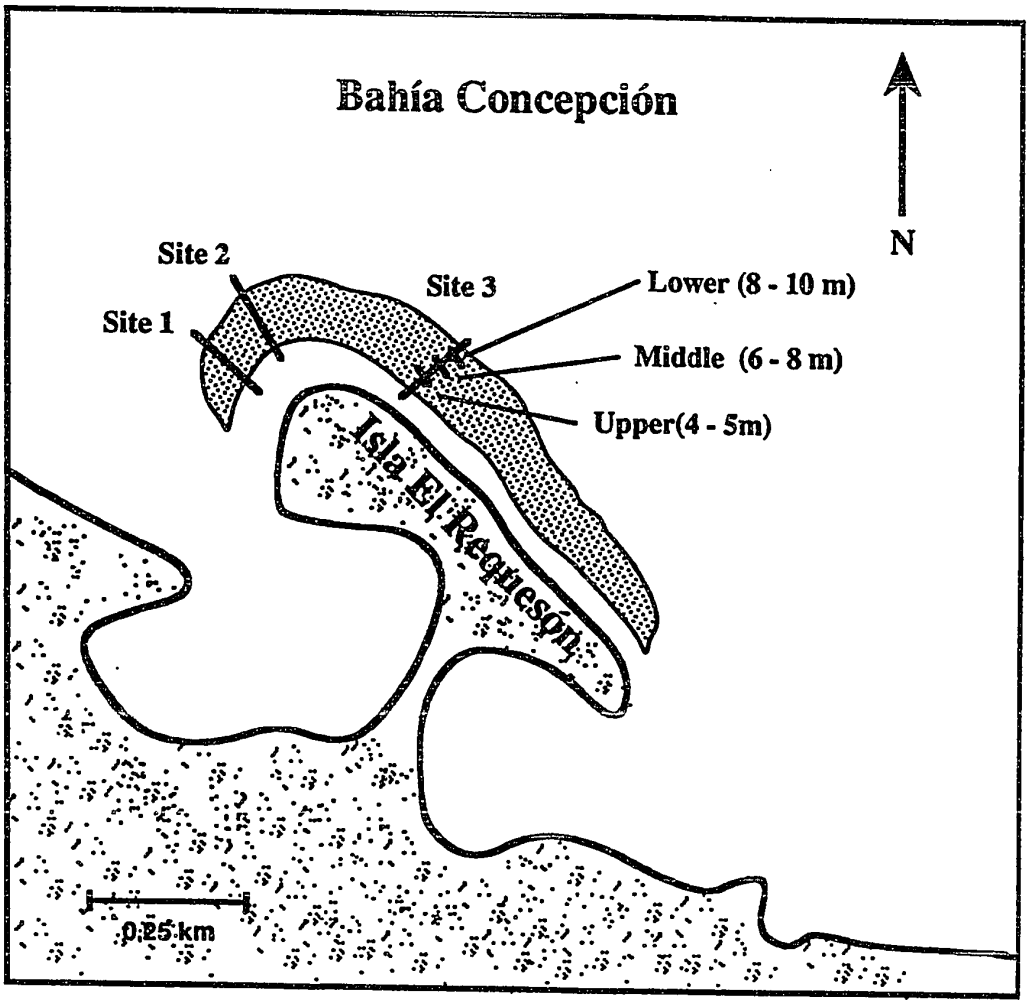

Bahía Concepción
N
Site 2
Site 1
Site 3
Lower (8 - 10 m)
Middle (6 - 8 m)
Upper(4 - 5m)
Isla El Requesón
0.25 km

Figure 4

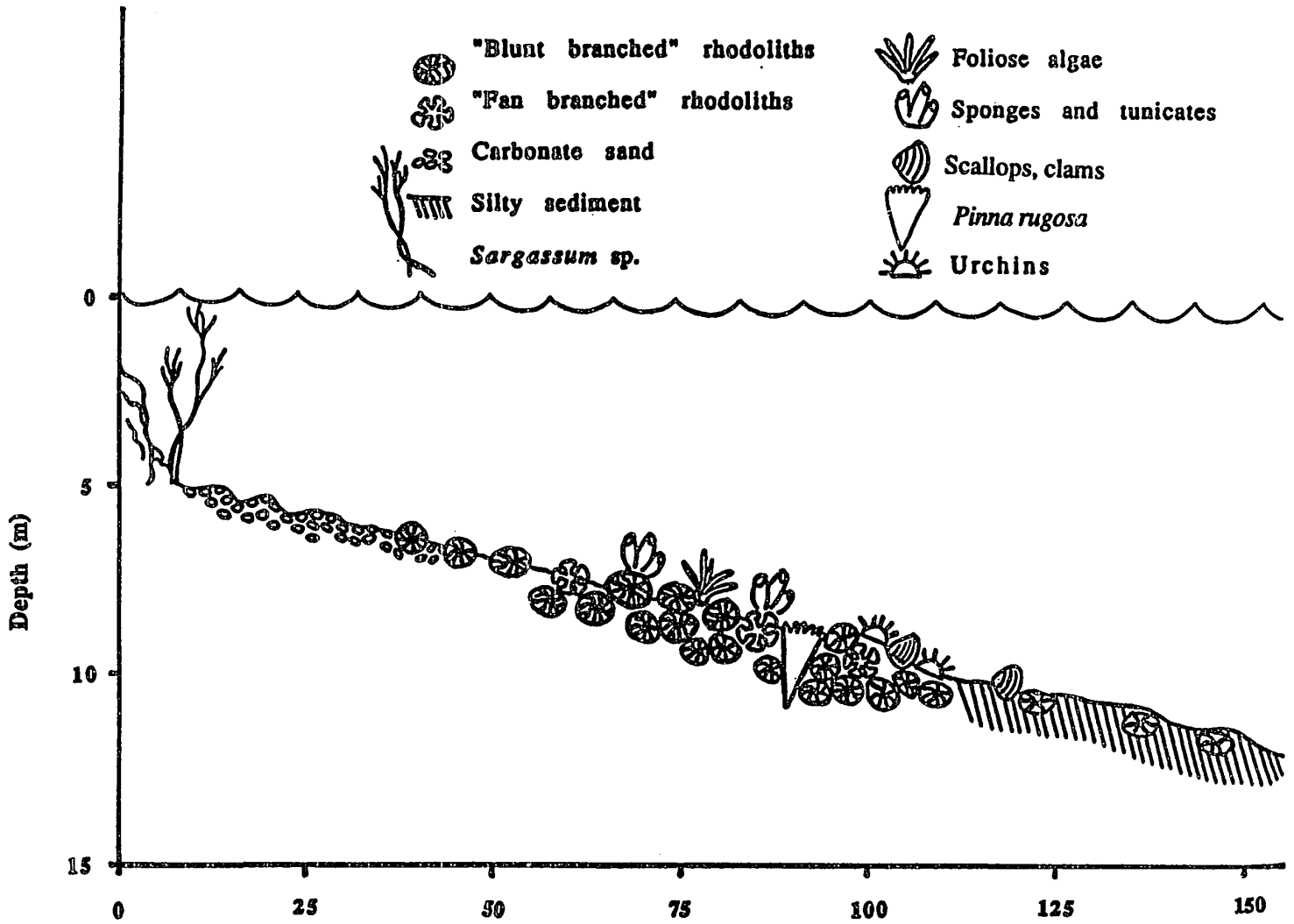

"Blunt branched" rhodoliths
"Fan branched" rhodoliths
Carbonate sand
Silty sediment
Sargassum sp.
Foliose algae
Sponges and tunicates
Scallops, clams
Pinna rugosa
Urchins
Depth (m)
0
5
10
15
0
25
50
75
100
125
150
Distance from shore (m)

Figure 5

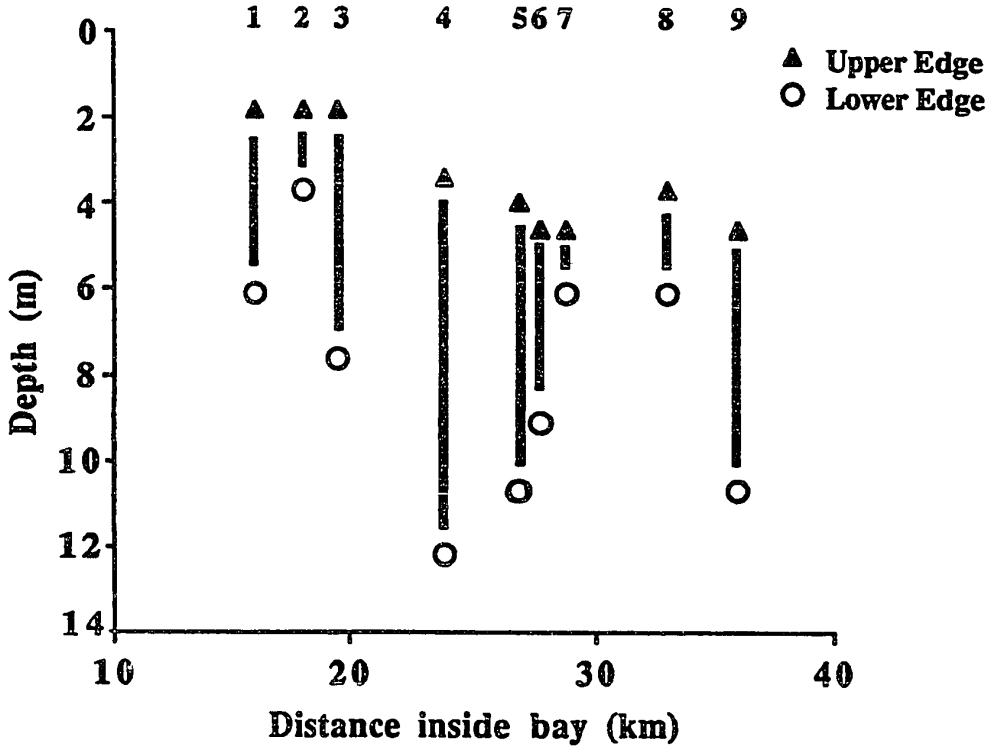

1 2 3 4 56 7 8 9
Upper Edge
Lower Edge
Depth (m)
0
2
4
6
8
10
12
14
10
20
30
40
Distance inside bay (km)

Figure 6

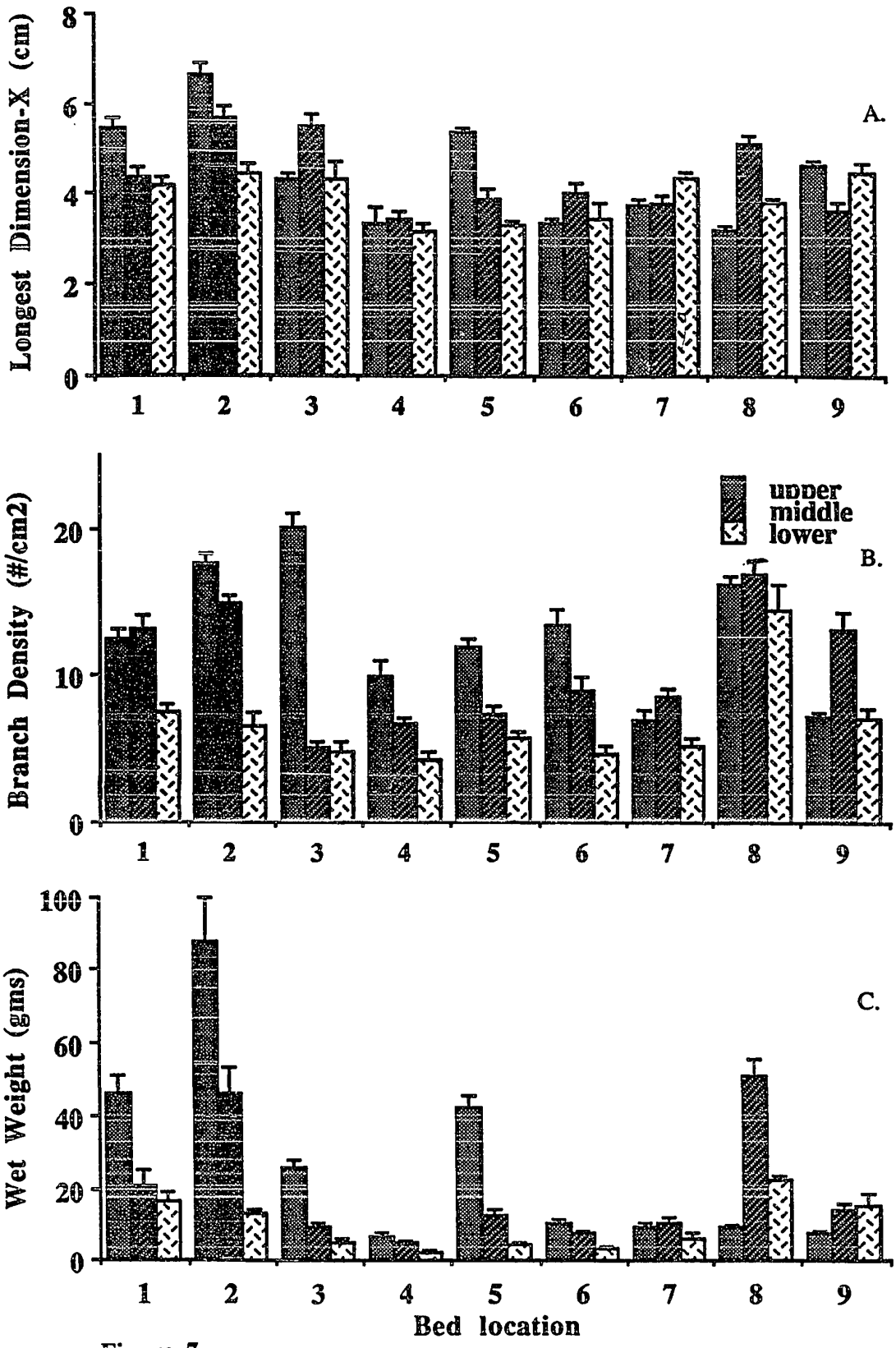

Longest Dimension-X (cm)
A.
Branch Density (#/cm2)
upper
middle
lower
B.
Wet Weight (gms)
C.
Bed location

Figure 7

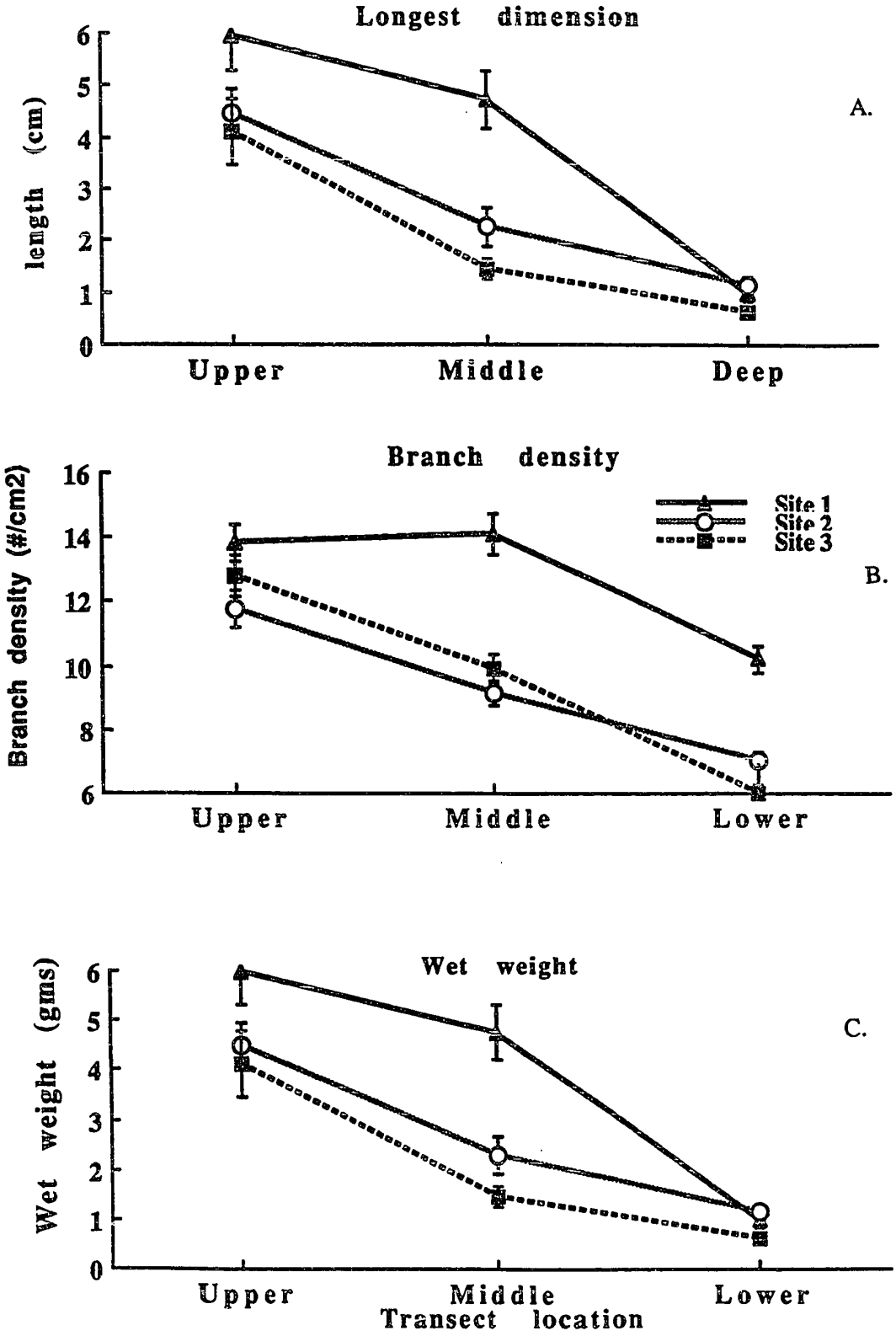

Longest dimension
length (cm)
6
5
4
3
2
1
0
Upper
Middle
Deep
A.
Branch density
Branch density (#/cm2)
16
14
12
10
8
6
Site 1
Site 2
Site 3
Upper
Middle
Lower
B.
Wet weight
Wet weight (gms)
6
5
4
3
2
1
0
Upper
Middle
Lower
Transect location
C.

Figure 8

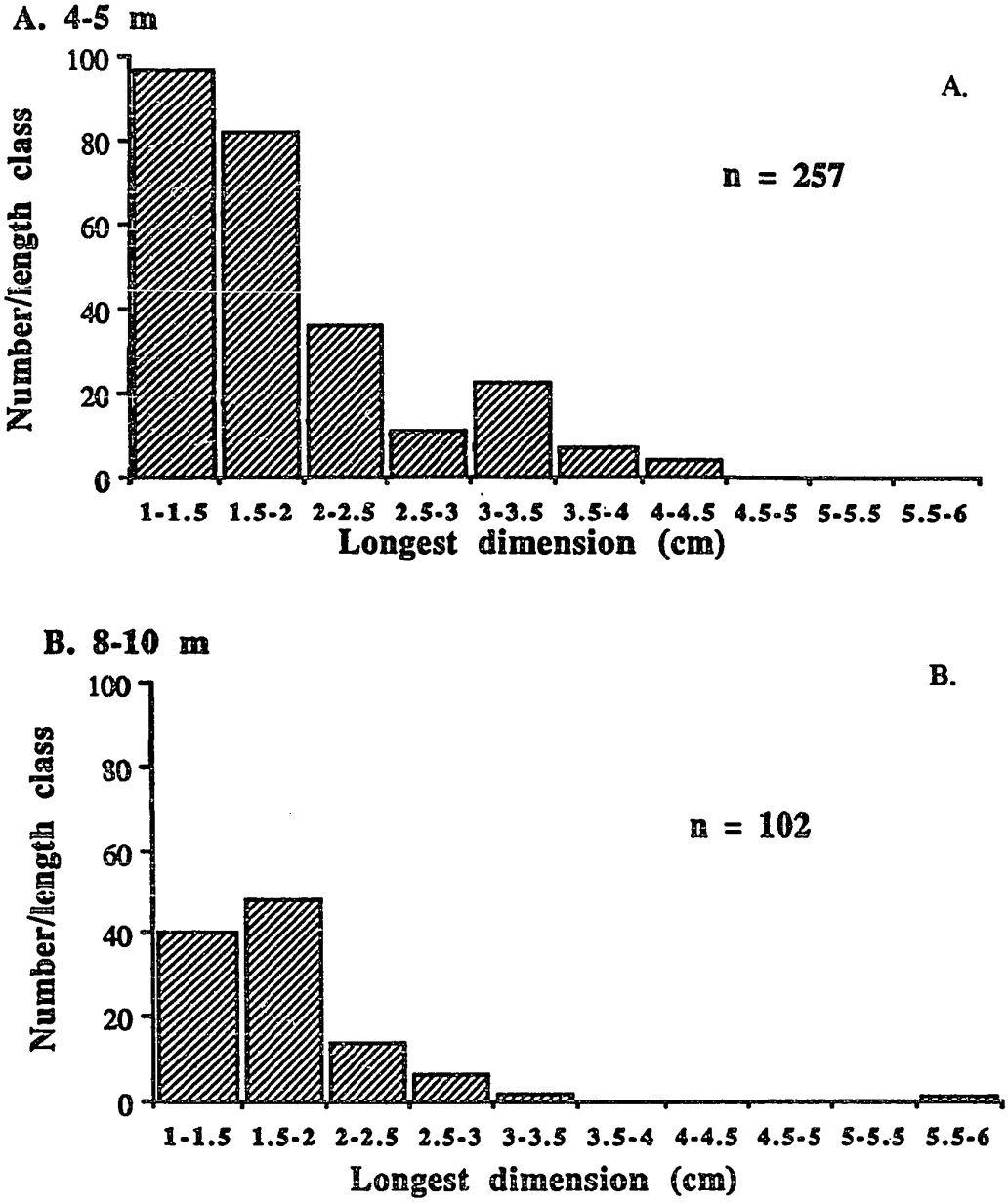
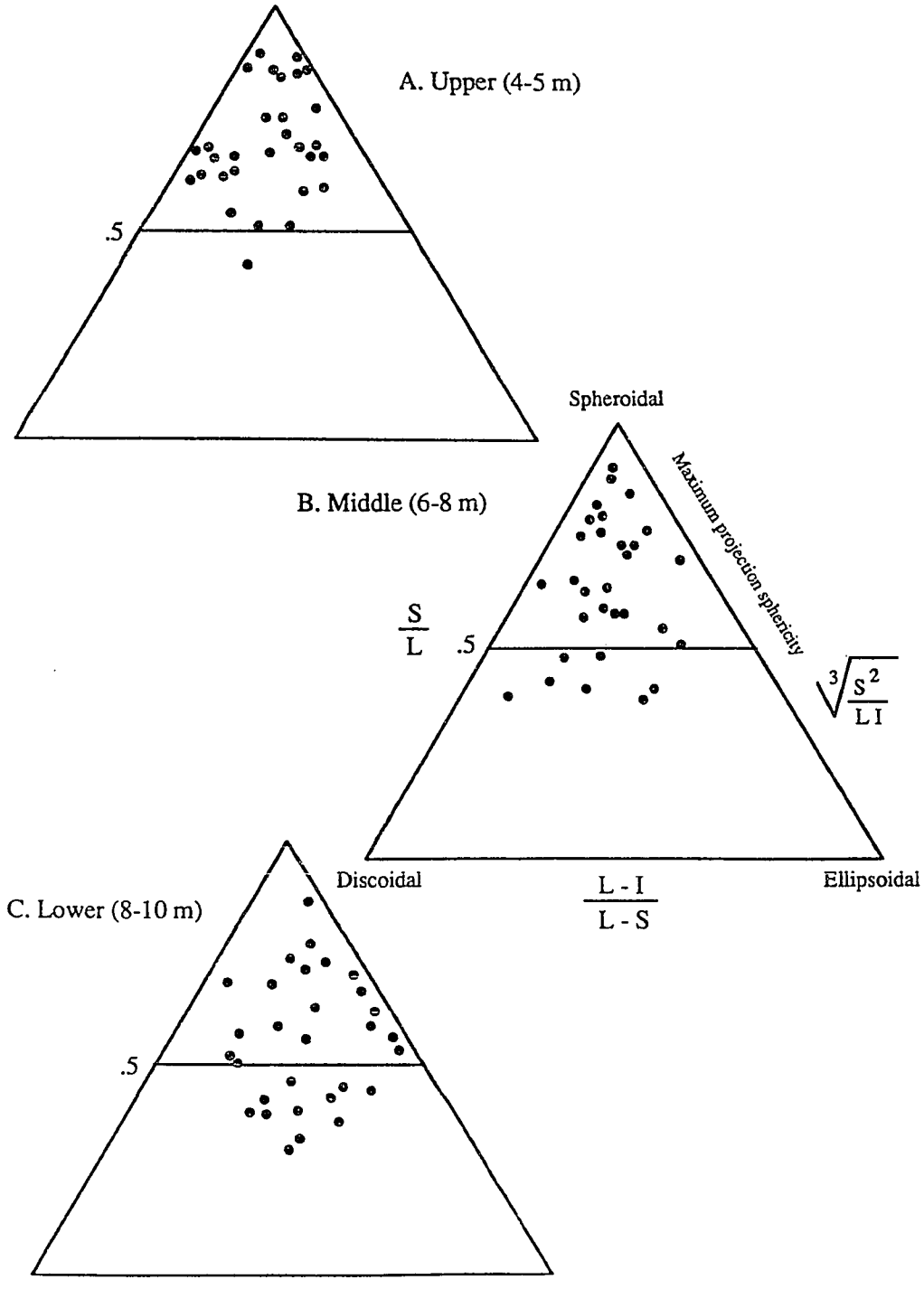

A. 4-5 m
A.
n = 257
Number/length class
100
80
60
40
20
0
1-1.5
1.5-2
2-2.5
2.5-3
3-3.5
3.5-4
4-4.5
4.5-5
5-5.5
5.5-6
Longest dimension (cm)
B. 8-10 m
B.
n = 102
Number/length class
100
80
60
40
20
0
1-1.5
1.5-2
2-2.5
2.5-3
3-3.5
3.5-4
4-4.5
4.5-5
5-5.5
5.5-6
Longest dimension (cm)

Figure 9


A. Upper (4-5 m)
.5
Spheroidal
B. Middle (6-8 m)
Maximum projection sphericity
$\frac{S}{L}$
.5
$\sqrt[3]{\frac{S^2}{L\,I}}$
Discoidal
$\frac{L-I}{L-S}$
Ellipsoidal
C. Lower (8-10 m)
.5

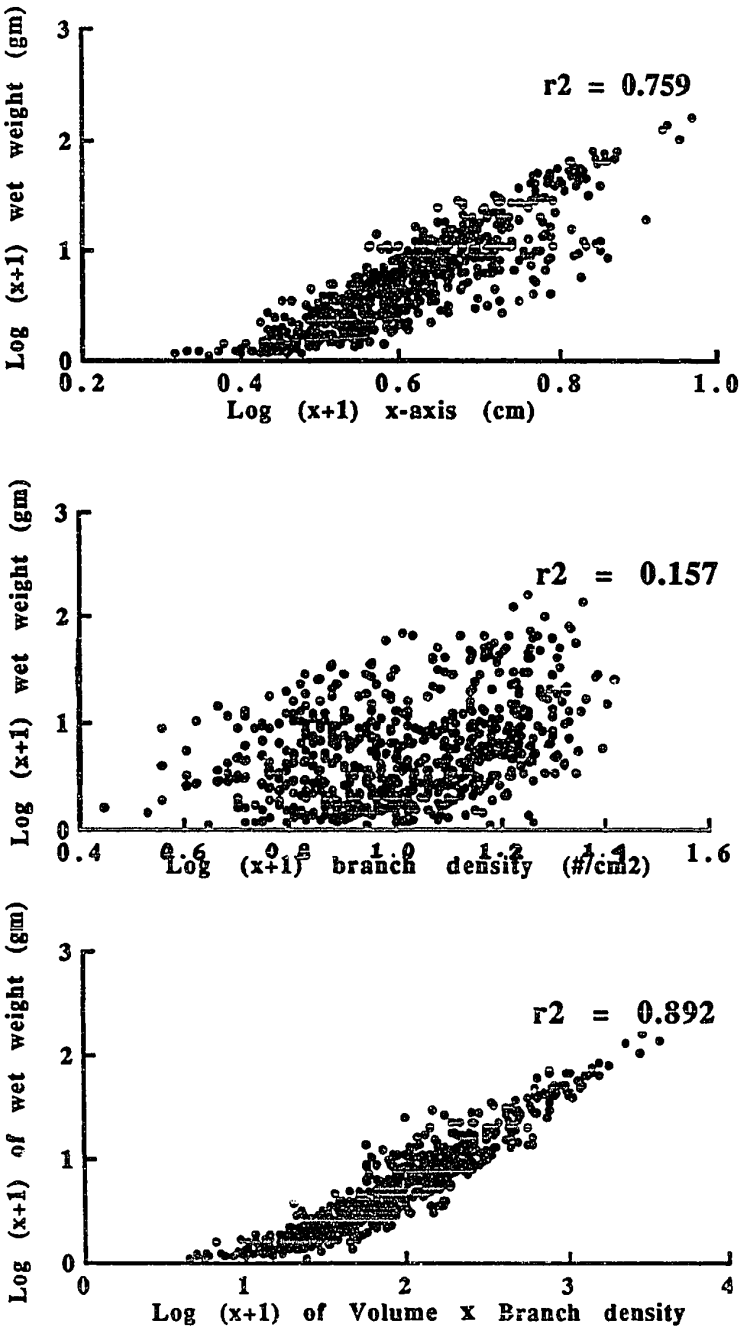

r2 = 0.759
Log (x+1) wet weight (gm)
Log (x+1) x-axis (cm)
r2 = 0.157
Log (x+1) wet weight (gm)
Log (x+1) branch density (#/cm2)
r2 = 0.892
Log (x+1) of wet weight (gm)
Log (x+1) of Volume x Branch density

Figure 11

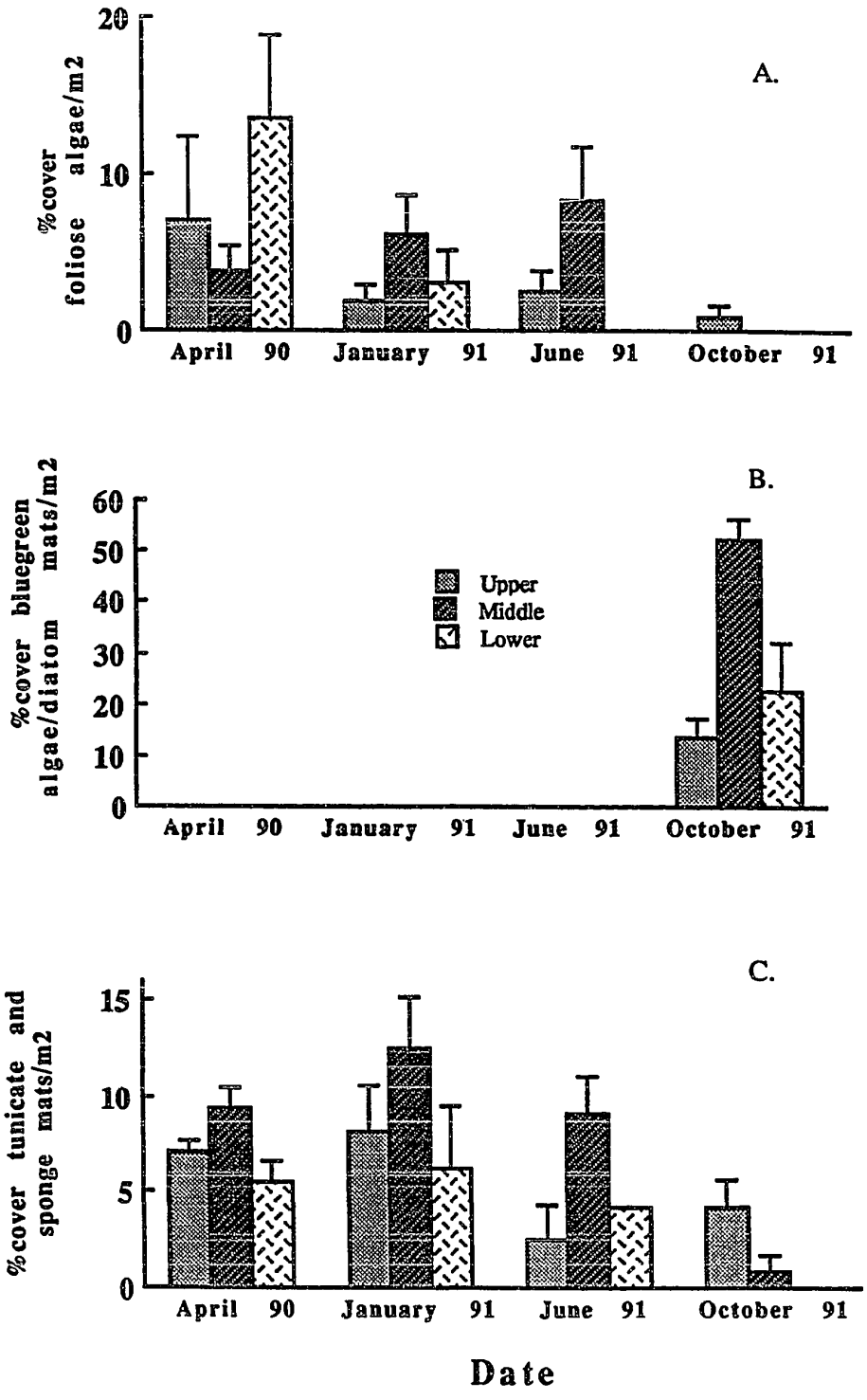

A.
%cover foliose algae/m2
20
10
0
April 90
January 91
June 91
October 91
B.
%cover bluegreen algae/diatom mats/m2
60
50
40
30
20
10
0
Upper
Middle
Lower
April 90
January 91
June 91
October 91
C.
%cover tunicate and sponge mats/m2
15
10
5
0
April 90
January 91
June 91
October 91
Date

Figure 12

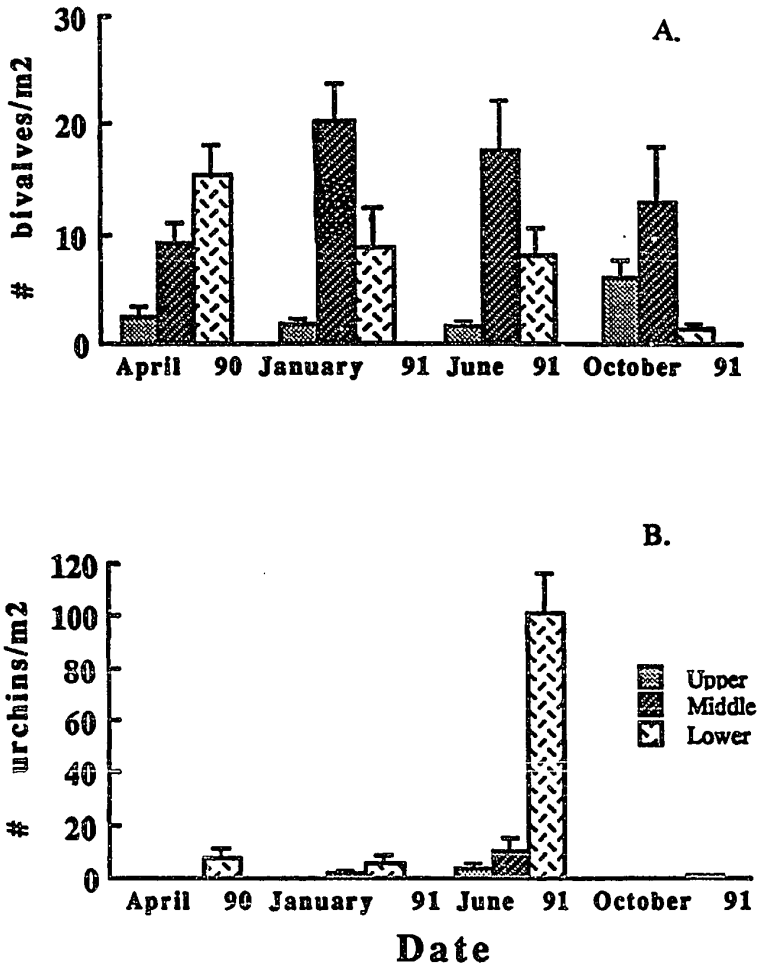
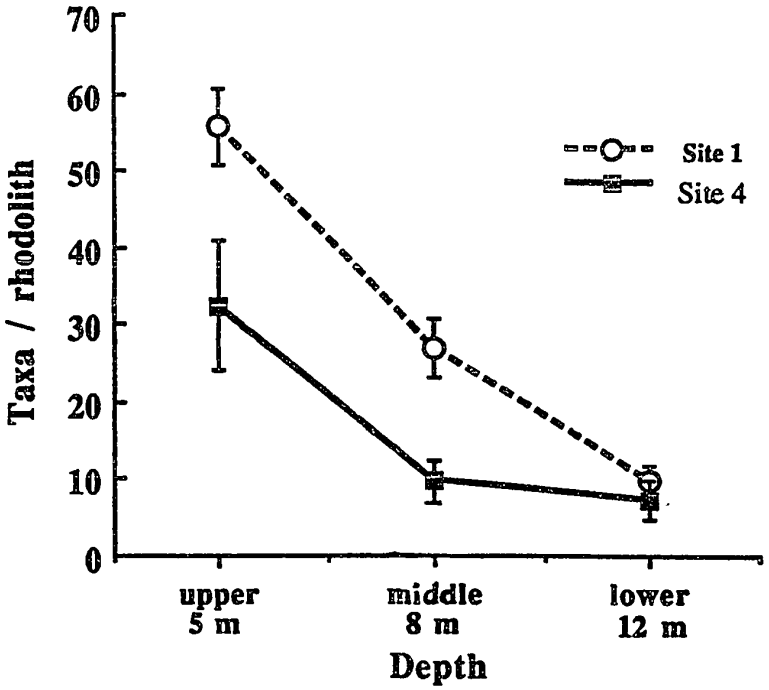

A.
bivalves/m2
30
20
10
0
April 90
January 91
June 91
October 91
B.
urchins/m2
120
100
80
60
40
20
0
Upper
Middle
Lower
April 90
January 91
June 91
October 91
Date

Figure 13


70
60
50
40
30
20
10
0
Taxa / rhodolith
Site 1
Site 4
upper
5 m
middle
8 m
lower
12 m
Depth

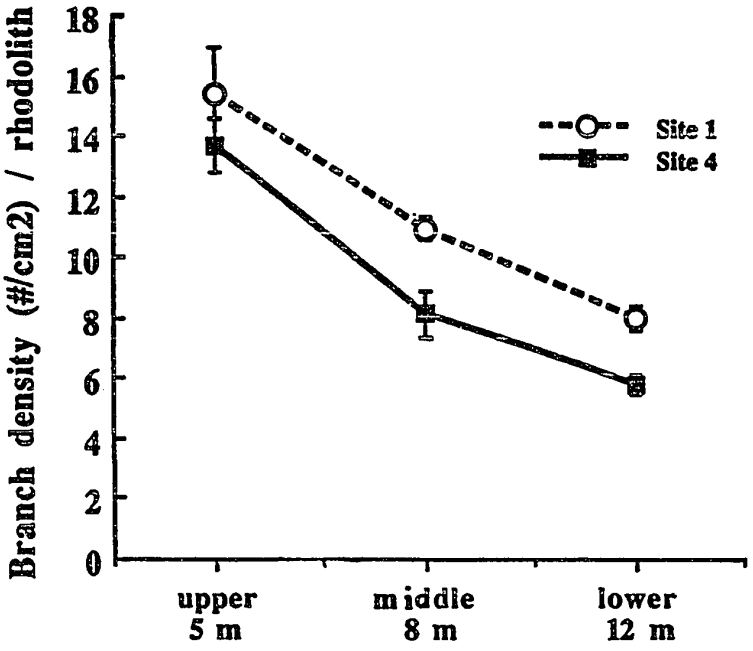

18
16
14
12
10
8
6
4
2
0
Branch density (#/cm2) / rhodolith
Site 1
Site 4
upper
5 m
middle
8 m
lower
12 m

Figure 14

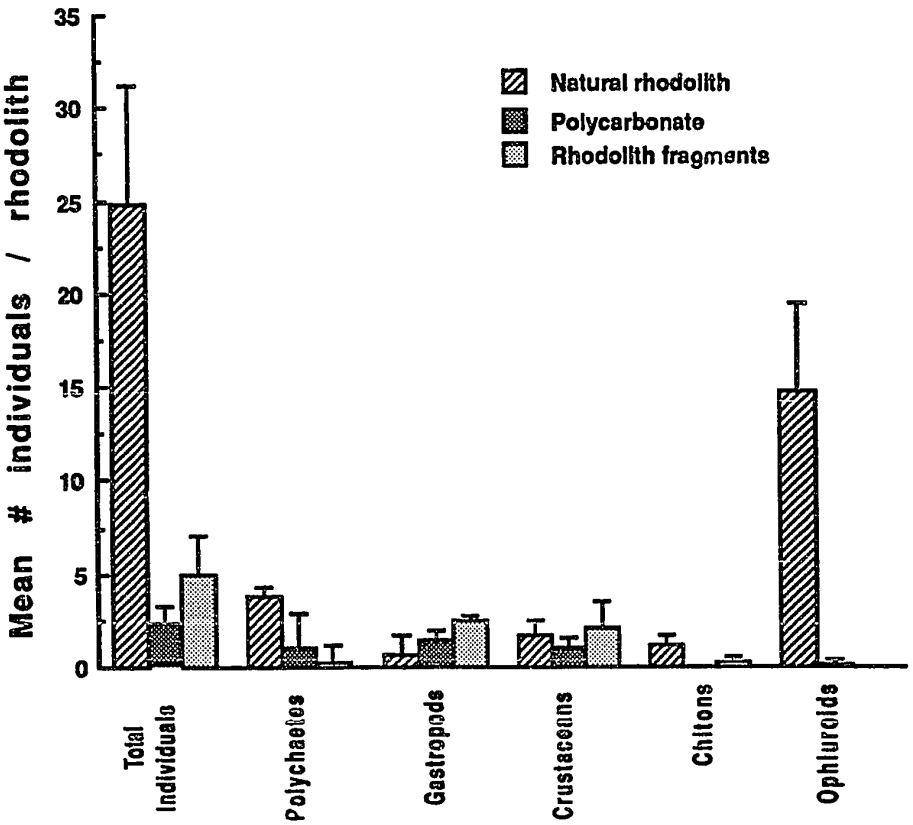

Mean # individuals / rhodolith
35
30
25
20
15
10
5
0
Natural rhodolith
Polycarbonate
Rhodolith fragments
Total Individuals
Polychaetes
Gastropods
Crustaceans
Chitons
Ophiuroids

Figure 15

Appendix

Species of plants and animals found associated with rhodoliths at Isla El Requesón and in Bahía Concepción during collecting trips in April 1990 and January, June, and October 1991. Common groups are divided into Epifaunal animals, Epifaunal plants, and Infaunal and Cryptofaunal animals. See Methods section for determination of these categories. Identifications were made to the nearest taxonomic level and number designations following the family names indicate the number of different species determined.

APPENDIX

A. EPIFAUNAL ORGANISMS

PORIFERA	
Lucetta cf. *losangelensis*	de Laubenfels
Aplysina fistularis	
G. Verigonia	(Bowerbank)
G. Haliclona	(Grant)
Acarnus erithacus	de Laubenfels
Tedania nigrescens	Schmidt
Hymeniacidon sp.	de Laubenfels
Desmacella sp.	
Tedania sp.	(Schmidt)
Dyridea sp.	(de Laubenfels)
Mycale - subgenus (Aegogrophila sp.)	(Duchassaing & Michelotti)
Leucetta cf. *losangelensis*	(de Laubenfels)
O. Haplosclerida	(Topsent)
CNIDARIA	
Anthozoa	
Antipathes galapagenisis	
Diadumene lineata	(Carlgren)
Haplanella luciae	(Carlgren)
Muricea sp. *californica*	(Aurivillius)
Pachycerianthus insignis	(Carlgren)
Porites californica	(Verill)
ECHINODERMATA	
Echinoidea	
Arbacia incisa	(A. Agassiz)
Echiometra vanbrunti	(A. Agassiz)
Eucidaris thouarsii	(Valenciennes)
Toxopneustes roseus	(Agassiz)
Holothuroidea	
Isotichopus fuscus	(Ludwig)
MOLLUSCA	
Class Bivalvia	
Arca pacifica	(Sowerby)
Argopectin circularis	(Sowerby)
Chione californiensis	(Broderip)
Chione tumrns	(Verill)
Chione undatella	(Sowerby)
Glycymeris gigantea	(Briderip)
Noetia reversa	(Sowerby)
Pinna rugosa	(Sowerby)
Sponydylus calcifer	(Carpenter)
Tivela planulata	(Broderip and Sowerby)
Trigoniocardia biangulata	(Kean)

Class Cephalopoda
Octopus digueti (Perrier & Rocheburne)

Class Gastropoda
Chromodoris galexorum (Bertsch)
Chromodoris norisii (Farmer)
Murex nigritus (Philippi)
Tridachiella diomedea (Bergh)

PLATYHELMINITHES
Marcusia ernesti (Hyman)

CHORDATA
Urochordata-
Aplidium sp. (Savigny)
Polyclinum laxum (Van Name)

B. EPIFLORAL ORGANISMS

RHODOPHYTA
O. Corallinales
Lithothamnium australe (Foslie) Foslie
Lithophyllum digueti (Hariot) Heydrich
Lithophyllum pallescens (Foslie) Heydrich
Lithophyllum margaritae (Hariot) Heydrich
Amphiroa misakiensis Yendo
Amphiroa rigida Lamouroux
Amphiora valonioides Yendo
Amphiroa van-bossaeae Lemoine

O. Ceramiales
Griffithsia pacifica (Kyl.)
Polysiphonia johnstonii Setchell et Gardner
Polysiphonia johnstonii var. *coccina* (Hollenberg) Hollenberg
Polysiphonia pacifica var. *delicatula* Hollenberg
Spyridia filamentosa (Wulfen) Harvey

O. Gigartinales
Gracilaria crispata Setch. et. Gardn.
Gracilaria subsecundata Setch. et. Gardn.

O. Nemaliales
Gelidiopsis tenuis Setch. et Gardn.

CHLOROPHYTA
O. Codiales
Bryopsis pennatula J. Agardh
Caulerpa vanbosseae Setchell et Gardner
Caulerpa sertularioides (Gmelin) Howe
Enteromorpha acanthophora Kützing

PHAEOPHYTA
O. Fucales
Sargassum sincola Setchell et Gardner
Sargassum herporhizum Setchell et Gardner

O. Dictyotales
Dictyota cf. divaricata Lamouroux
Padina durvillaei Bory

O. Scytosiphonales
Chnoospora implexa Hering et. J. Agardh
Colpomenia tuberculata Setchell et Gardner
Hydroclathurus clathratus (C. Ag.)
Rosenvingea intricata (J.Agardh) Børgenson

C. INFAUNAL AND CRYPTOFAUNAL ORGANISMS
( ) = number of different unidentified species per family

ECHINODERMATA
Cl. Ophiuroidea
F. Ophiochitonidae
Ophiactis savignyi LeConte
F. Ophiactidae
Ophiothrix spiculata LeConte

ANNELIDA
Cl. Polychaeta
F. Terebellidae (2)
Pista elongata Moore
F. Nereidae (4)
F. Phyllodoicidae (2)
F. Syllidae (1)
Typosyllis sp.
F. Lysaretidae (1)
Oenone fulgida (Savigny)
F. Polynoidae (1)
F. Sabellidae (1)
F. Cirratulidae (1)
F. Pectinariidae (1)

ARTHROPODA
F. Amphipoda
Elasmopus rapaxmutatus Barnard
F. Isopoda
Excerallana kathyae Menzies
Haliophasma geminata Menzies & Barnard
Jaeropsis dubia Menzies
F. Tanaeidae (1)
F. Ostracoda (1)

MOLLUSCA
Class Bivalvia
Lithophaga aristata Dillwyn

Class Gastropoda
F. Acmaeidae (1)
F. Olividae (1)
F. Turbinidae (1)
F. Acteocinidae (1)
F. Cerithiidae (1)

Class Polyplacophora (1)
Acanthochitona avicula Brusca
Ischnochiton cyanomaculatus Putman

CNIDARIA
Class Anthoza
Diadumene lineata Carlgren
Haplanella luciae Carlgren